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A NEW LUGWORM FROM WOODS HOLE, HITHERTO INCLUDED IN *ARENICOLA CRISTATA* (POLYCHAETA)

BY

G. P. WELLS

Department of Zoology, University College, London

[Accepted 14th February, 1961]

(With 4 plates and 2 figures in the text)

The Woods Hole fauna contains two distinct species, both conforming to the current diagnosis of *Arenicola cristata* Stimpson. In the absence of Stimpson's original material, one of them is identified with his species on the basis of his descriptions. The other is described as *Arenicola caroledna* sp. nov. Their distinguishing characters have not previously been regarded as of taxonomic importance so it is often impossible to tell from the literature alone whether a record of "*Arenicola cristata*" refers to *cristata* in the strict sense, to *caroledna* or even perhaps to some other form.

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In fact, as has been suspected locally for some time, there is also a third, for the current definition of Stimpson's species really includes two forms and both are present in the area. The following paper reports on a comparison of the latter two, as they are seen at Woods Hole.

One of the forms to be compared is the large, dark-coloured worm used for dissection every year by the Invertebrate Class at the Marine Biological Laboratory. The other is smaller, much lighter in colour and more delicate in appearance and "feel". In the descriptive paragraphs, the former will be called *cristata* and the latter *caroledna*; the taxonomic status of the forms is discussed at the end.

The former is by far the better known. The earliest evidence, as far as I know, for the presence of *caroledna* in the area is a small group of specimens in the private collection of the late Professor J. H. Ashworth, which is now in my hands. The specimens were collected at Woods Hole by Ashworth himself in 1930 and as he also preserved and kept some of their characteristic egg masses, we may suppose that he suspected that they were different from *cristata*. Its existence was noticed by myself when visiting Woods Hole in 1936 and I have studied it there on several subsequent occasions. Many specimens of *caroledna* have been collected and important observations on its behaviour and distribution in the area have been made by Mr Milton Gray of the Marine Biological Laboratory and by Drs George Moore and Marian Pettibone of Durham, New Hampshire. All of these colleagues have generously placed information and material at my disposal.

ANATOMY OF *A. CAROLEDNA* AND *A. CRISTATA*

The two forms can generally be distinguished at a glance, even after hasty preservation. *A. cristata* is a massive worm, commonly reaching a considerable length; it was a specimen of this form which Ashworth (1912) described as "a veritable giant among Polychaeta, as it had attained a length of 515 mm. (the tail was 190 mm. long) and a girth of 75 mm.". In the following paper the lengths are given exclusive of tail, to eliminate arbitrary variations due to autotomy or accidental breakage of that fragile part of the body. *A. cristata* probably grows up rapidly, for, although small individuals are sometimes found, the great majority of those one sees fall in the range 150 to 300 mm. when killed in a reasonably relaxed or extended attitude, for example by formalin after magnesium chloride narcosis. *A. caroledna* is smaller; the largest I have seen measured 173 mm.

A. cristata is a deep brown-black colour with a striking bottle-green fluorescence. *A. caroledna* is paler—pinkish white or pinkish tan with a variable amount of brown pigment, especially in the more anterior segments. It never approaches the dark green-black of *cristata*.

The living worms feel quite different when held in the hand. Healthy *cristata* are firm and turgid, while *caroledna* are soft and limp; yet both can burrow away rapidly when placed on sand. A person familiar with living lugworms of other species might suppose the limp-bodied *caroledna* to be unhealthy, before he saw how vigorously they can dig.

Segmentation

In both *cristata* and *caroledna* there are normally 17 setigers, and the most anterior gill (which may be small or absent) is on the seventh. As in other lugworms, occasional individuals of both species show anomalies of segmentation at the junction of trunk and tail (e.g. one or two appendages of setiger xvii missing, or extra appendages present representing an incomplete eighteenth setiger).

Gills

Both forms have pinnate gills. Those of *cristata* look rather shorter and bushier, and those of *caroledna* relatively longer and more elegantly pinnate, but the gills are highly contractile and these differences are hard to define with precision.

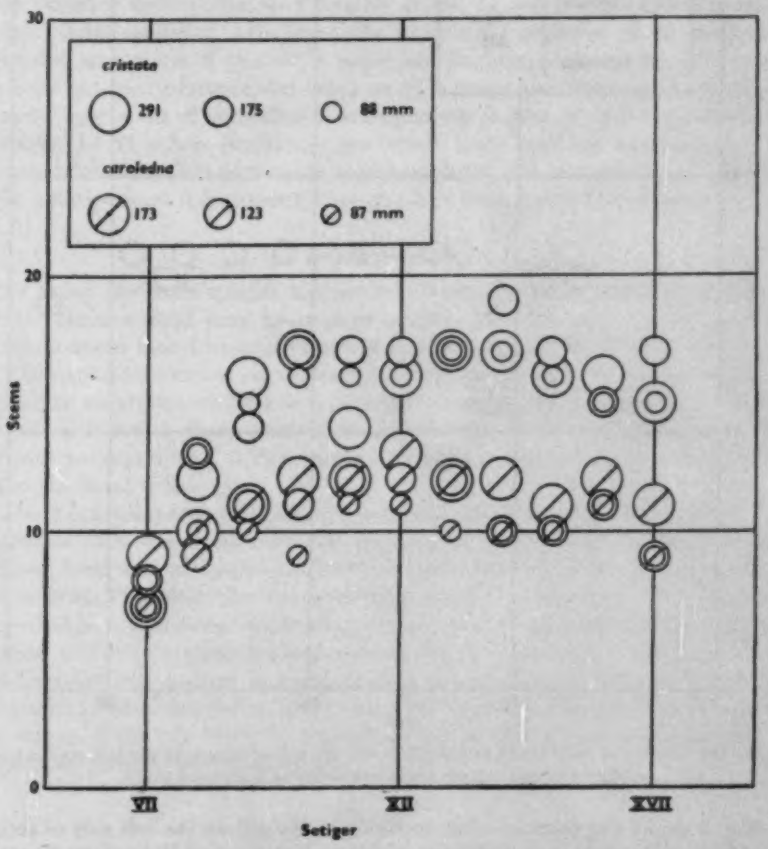

Fig. 1—The number of main stems per gill in all of the gills of the left side of three specimens of each species. The lengths of the specimens are given exclusive of tail.

The two forms differ in the number of main stems, i.e. of those stems which radiate out through the basal web, like fingers radiating through the palm of the hand. The main stems of any gill may differ greatly in size, those of the ventral end being generally very small. The following paragraphs concern the total number irrespective of size.

Fig. 1 shows the number of main stems in each gill on the left side of the body. This information is given for three individuals of each form, chosen to give widely overlapping size ranges (*cristata* 88, 175 and 291 mm., *caroledna* 87, 123 and 173 mm., all exclusive of tail). It will be seen that the number of gill stems is consistently greater in *cristata* if we overlook the first two branchiate setigers (vii and viii), whose gills are smaller than the rest.

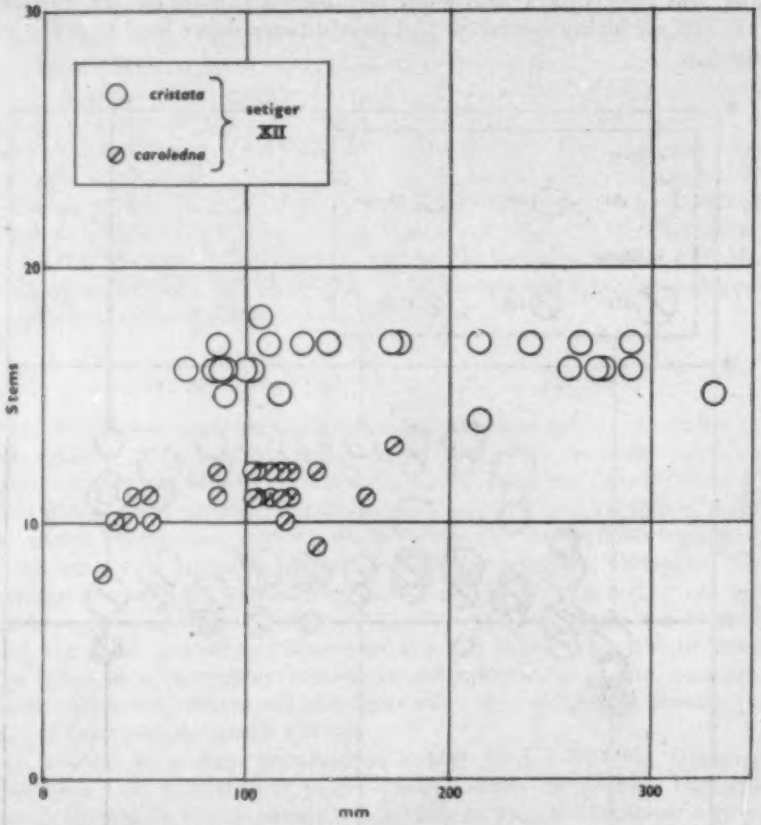

Fig. 2—The number of main stems in the gill on the left side of setiger xii plotted against length exclusive of tail. Each circle represents an individual worm.

Fig. 2 shows the number of main stems in the gill on the left side of setiger xii. Each point is from a different worm, and stem number is plotted against tailless length. It is clear from this graph that the number of stems depends

on the form and, except perhaps for the smallest *caroledna*, is independent of size over the size range of the available specimens. The number of main stems counted in gill L. xii ranged from 8 to 13 in *caroledna* and from 14 to 18 in *cristata*. The commonest numbers are 11 or 12 in *caroledna* and 16 or 17 in *cristata*.

We may note in passing that although the number of gill stems serves to emphasize the distinctness of the two forms at Woods Hole, it is not always a reliable character for distinguishing specimens from other parts of the world. Details on this point will be given in a later paper.

Notopodia and neuropodia

Like the gill stems, the notopodia are proportionately smaller in *cristata* than in *caroledna* (Plate 1).

In both forms, there is a tendency to reduction and disappearance of the more anterior neuropodia, and *cristata* seems to carry the reduction rather further than *caroledna*. On carefully examining a series of 15 artificially distended specimens of *cristata*, I could see no neuropodia on setigers i or ii, the most anterior neuropodium being on iii in some specimens and iv in others. In some specimens of *caroledna* a neuropodium is plainly visible on each side of setiger i ; in others (including one whose body wall has been cleared and mounted flat on a slide to remove any possible doubt) neuropodium i is absent while neuropodium ii is present, though often minute, on both sides.

Nephridiopores

In many lugworm species the nephridiopore is a plain dorsi-ventral cleft, but in others a hood may be present outside the true nephridiopore, which therefore opens into a more-or-less well-defined atrium (Healy & Wells, 1959).

The nephridiopores of *caroledna* are fully hooded. The true nephridiopore opens into an atrium which is seen externally as a slightly raised area, prolonged ventralwards into a sharp point that extends well below the upper end of the adjacent neuropodium. Urine escapes through a round hole near the dorsal end of the hood (Plate 1).

The nephridiopores of *cristata* are rather more variable. Typically, the nephridial cleft opens on a special pentagonal area whose texture is rather different from that of the general body surface ; the ventral hood is very small, so that most of the cleft (the true nephridiopore) is exposed (Plate 1). Occasionally—that is, in occasional nephridiopores, not occasional individuals—the hood is larger and may approach the condition seen in *caroledna*. But even when this happens, the atrium is more pentagonal in *cristata*, without the acute downward point of *caroledna*, and in practice there is little difficulty in separating worms of the two kinds by inspecting the nephridiopores alone, as long as the surface preservation is adequate.

The tail

The lugworm tail is renewed by backward growth from reserve segments at the base. Generally it consists of many segments, the hindmost ones being

of course the longest. In large *cristata*, however, there may be few tail segments —7 to 10, according to Ashworth (1912)—and this is apparently due to exhaustion of the supply of reserve segments (Wells, 1950). In *caroledna*, on the other hand, the tail always comprises many segments unless it has obviously been broken off. This difference between the two forms is less impressive when one compares small *cristata* with *caroledna* of similar size, and I am inclined to regard the short tails of large specimens of *cristata* as a secondary result of their size and their probably longer life.

The tails of both forms show the "hollow thumb-shaped processes" mentioned by Ashworth (1912, p. 109).

Internal anatomy

The two forms resemble each other in visceral segmentation. They have six pairs of nephridia, opening on setigers v to x. The plane of septum vi (at the hinder boundary of setiger vi) is the heart plane—that is, although the septum itself has degenerated, its commissural vessel is enlarged to form the hearts. The dorsal septal vessel ("efferent branchial" of Ashworth, 1904)—another derivative of the septal commissures—runs from the gill to the subintestinal vessel in the more anterior of the branchiate segments but to the dorsal vessel in the hinder ones, the "dorsal septal change" taking place between septal planes x and xi (Plate 2).

Occasional individuals of *cristata* have extra nephridia at the hind end of the series. Gamble and Ashworth (1900, fig. 30) show one with a nephridium on the right side of setiger xi. The students of the Invertebrate Class at Woods Hole in 1959 were asked to look out for anomalies while dissecting *cristata* and two worms with a nephridium unilaterally on xi were reported out of thirty-nine dissected. I have a specimen with small nephrostomial funnels (not complete nephridia) on both sides of xi and the left side of xii. This kind of anomaly has not yet been reported in *caroledna*, but as that form is not a classroom type the number so far dissected is considerably less.

In both forms, the septal pouches are substantially larger than in *A. marina* (Plate 3; compare Ashworth 1912, Wells 1952).

There are several differences in the proportions of the organs, between *cristata* and *caroledna* (Plate 2). Most striking are the differences in the nephridia, and especially the nephrostomes. The nephridial funnel of *caroledna* is relatively much the larger, with the vascular processes of the so-called dorsal lip fewer but individually more prominent (lower halves of Plates 3 and 4).

The position of the nerve cord

This is a character to which I attach considerable importance, although it has not generally been used in arenicolid taxonomy. It can easily be seen, in adequately preserved material, by making a transverse snip in the ventral body wall of one of the branchiate segments and looking at the cut surface with a binocular dissecting microscope.

The position of the nerve cord relative to the muscle layers of the body wall varies in different lugworm species. The most primitive condition is found in

Abarenicola claparedii and *Abarenicola vagabunda*; the nerve cord in those species is in contact with the epidermis and wholly outside the circular muscle layer. In *Abarenicola assimilis* and *Arenicola marina*, and also in the two species of the ecaudate genus *Arenicolides*, the nerve cord lies deep to the circular muscle layer and in the plane of the longitudinal layer, which it interrupts.

The latter condition is found also in *caroledna*; here the nerve cord lies deep to the circular muscle layer and separated from it by a small cavity (Plate 4). In *cristata*, on the other hand, there is a condition which I have seen elsewhere only in *Arenicola loveni*; the longitudinal muscle has closed in behind the centripetally migrating nerve cord, so that there is longitudinal muscle between the cord and the circular muscle layer. The interannular nerves to the body wall therefore have to make their way through the longitudinal muscle to reach the level, on the deep face of the circular layer, at which they run around the body (Plate 4).

The nerve cord presumably reaches this position by passing through a series of stages corresponding to the ones described above, in the course of individual development. The process must occur early, for the position of the nerve cord has been checked in numerous specimens, the *cristata* ranging from 71 to 292 mm. in length and the *caroledna* from 30 to 173, all lengths exclusive of tail. There was longitudinal muscle between the nerve cord and the circular muscle layer in all of the *cristata*, but in none of the *caroledna*.

Statocysts

In both *cristata* and *caroledna*, the statocysts are closed, each containing a single, secreted statolith made up of concentric layers. The form of the statolith is roughly that of a biconvex lens, so its outline appears ovoid or lenticular in some aspects and circular in others.

The histology of the skin

Mention was already made of the difference in "feel" between living worms of the two forms. I examined sections of various parts of the body wall, to find an explanation for this difference. To exclude any possibiltiy that the great histological contrast shown by the body walls of the two forms is dependent on size, I studied worms of the following lengths exclusive of tail: *cristata* 71, 100, 190, 275 mm.; *caroledna* 30, 53, 75, 136 mm. The histological picture was the same, in all the worms of either form.

The histology of the epidermis in the branchiate segments is strikingly different in the two forms (Plate 4, upper half). That of *cristata* has the usual appearance of a lugworm epidermis, while that of *caroledna* consists almost, entirely of a palisade of mucous cells staining a clear blue colour with Mallory's triple stain. In the more anterior segments, the mucous cells are less abundantly developed, but here, too, they are more conspicuous in *caroledna* than in *cristata*.

On the other hand, the musculature is rather more robust, and the connective tissue between the layers of the body wall is better developed, in *cristata* than in *caroledna*.

The enormous development of mucous cells in the epidermis of *caroledna* has the consequence that specimens of this form, unlike most lugworms, keep very badly in formalin, their body surface becoming swollen and soft. Preservatives containing spirit are satisfactory.

ECOLOGY OF *A. CAROLEDNA* AND *A. CRISTATA*

The surface signs, by which the presence of the worms can be recognised in the Woods Hole area, are very different in the two forms.

A. caroledna makes abundant cylindrical castings, of the type commonly produced by other lugworms. Its egg masses are gelatinous, fairly firm to the touch, spherical or egg-shaped with a distinct narrow stalk running down into the head shaft of the burrow. They measure about 40 to 75 mm. across, in the rounded part.

A. cristata has never been seen to produce a cylindrical casting, in the field or in the laboratory. Instead, it smears its faecal sand in films, around the caudal opening of the burrow or inside the burrow wall. Its egg masses are much larger than those of *caroledna* ; it is *cristata* that makes the gelatinous streamers, up to a metre in length and several centimetres in diameter, that so many authors have described. These streamers are looser in texture and less regular in form than the egg masses of *caroledna*. One end tapers slightly and is anchored in the head shaft, but there is no clearly differentiated stalk.

The two forms are nearly always found on separate beaches. *A. caroledna* shows an apparent preference for sand. *A. cristata* is generally in muddy sand, and, in the words of a letter to myself from Mr Milton Gray, " although at times we have found them fairly abundant in quite exposed places, they do seem to prefer inner waters and salt water ponds with salt water marshes nearby ". Occasionally they are found together, for instance on the beach inside Chappaquoit Point, West Falmouth, in 1954, where the two forms of egg masses could be compared.

The distributions, especially of *caroledna*, vary greatly with time, even when there is no obvious change in the nature of the beach. In the mid-thirties and forties, *caroledna* was abundant at several places in the Elizabeth Islands, for example at Hadley Harbor, but now it has deserted most of these stations and is only to be found at Cuttyhunk, where it occurs on the flats in the harbour at extreme low water. There is a possibility that its presence in the intertidal zone may be seasonal. Mr Milton Gray found no indications of the presence of *caroledna* at Cuttyhunk in May, 1960 ; castings were absent, and random digging revealed neither worms nor burrows. He revisited the station on 7th August and wrote in a personal communication : " The mounds of castings at Cuttyhunk at this time were much more numerous than I have seen them for years. The oval egg sacs were also numerous. This was at the same spot where I saw no indications of mounds last spring." It may be that the worms were present, but dormant, in May. On the other hand, they may have retreated beyond the littoral zone for the cooler months, as certain Japanese worms, which I regard as belonging to the same species, are said to do (Takahashi, 1934).

A. cristata, which seems to prefer the soft, muddy sand of estuaries, is becoming scarce in many places. This may be due, at least in part, to the continual dredging of harbours and channels.

TAXONOMY OF *A. CAROLEDNA* AND *A. CRISTATA*

The observations described above, on the anatomy and biology of the two forms as they are found in the Woods Hole area, leave little room for doubt that they are specifically distinct. They are clearly distinguishable by a number of anatomical characters. No intermediate individuals have been seen, and even when the two are found living side by side on the same beach, they retain their distinct egg-mass shapes and casting habits. The fact that both conform to the currently accepted diagnosis of *Arenicola cristata* means only that current critera, based largely as they are on the study of preserved worms in collections, are incorrect.

If this conclusion be accepted, two questions of nomenclature arise. The first : Can either form be identified with the material which Stimpson named in 1856 as *Arenicola cristata* ?.

Stimpson's original specimens no longer exist. According to Ashworth (1912) they were " in all likelihood destroyed with the Chicago Academy of Sciences in the great Chicago fire ". Fortunately, however, his description allows of a decision. His worms were collected from hard sand covered with a deposit of mud on the shore of Maurice Island, at the entrace to Charlestown Harbor, South Carolina. They were large—up to 16 inches long by 1 inch thick. Their colour was " rich, dark green of various shades, often approaching to brown in the middle of the body ". They produced " great quantities of a soft, transparent jelly filled with minute brownish specks, which proved to be eggs ". Very significantly, Stimpson made no mention of faecal cylinders, although he described the burrows in detail. In every ascertainable respect, then, his worms agreed with the form here called *cristata*, which is therefore *Arenicola cristata* Stimpson.

The second question : has another name ever been given to specimens of the new form ? Here a possibility is *Arenicola antillensis* based by Lütken (1865) on material from St Croix, in the West Indies, and shown by Horst (1889) and by Fauvel (1899) to agree with the then-current diagnosis of *A. cristata*. I recently re-examined Lütken's type, which is in the Universitetets Zoologiske Museum at Copenhagen, and find that it agrees completely with the form here called *cristata* ; so *antillensis* Lütken is still a synonym of Stimpson's species. Nonato (1938) described a " var. *brasiliensis* " of *A. cristata*, distinguished by certain peculiarities of the statocyst. This is in fact a local variety of *A. caroledna*, as I shall show in a later paper. A varietal name has however no status in formal taxonomy and therefore no right of priority as a species name ; this is as well, for it would be inappropriate to attach a local name to a species which, as will be shown, has a very wide distribution. No other published names present themselves.

A name is therefore required by the new species, and *Arenicola caroledna* has been coined for this purpose, in commemoration of the two spectacular

hurricanes which visited Woods Hole while the form was under investigation there in 1954, and were known to the meteorologists as Carol and Edna.

DIAGNOSES

Below are a diagnosis of the new species, and a revised one of the old. Geographical distributions cannot yet be given, for the following reason. The characters distinguishing the worms have not previously been regarded as of taxonomic importance. It is therefore impossible, in most cases, to decide from the literature whether a published record of "*A. cristata*" should be referred to *cristata* in the strict sense, to *caroledna*, or perhaps to some other form. At the present time, I am examining specimens of "*A. cristata*" from as many points as possible in the very extensive range of distribution of that supposed species, and expect to report on the results in due course.

Arenicola cristata Stimpson 1856.

Arenicola antillensis Lütken 1865.

Arenicola with 17 setigers. Gills 11 pairs, on setigers vii to xvii. Nephridia 6 pairs, opening on setigers v to x. Inner end of dorsal septal vessel moves from subintestinal to dorsal vessel in setiger xi. Septal pouches large. Oesophageal glands comparatively short. Statocysts closed, each with a large, secreted statolith. Nerve cord deep to the longitudinal muscle layer.

The original material, from Charlestown, South Carolina, no longer exists. The type of *Arenicola antillensis* Lütken, from St. Croix, West Indies, is in the Universitetets Zoologiske Museum at Copenhagen.

Arenicola caroledna sp. nov.

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Holotype (coll. Gray, at Cuttyhunk, August 17 1958) in the British Museum (Natural History), Catalogue number 1961 : 1 : 1. Paratype, from the same batch of material, in the U.S. National Museum, Washington.

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EXPLANATION OF THE PLATES

All animals shown are from the Woods Hole collecting area. The lengths of the worms, as given in millimetres in the Plates, are exclusive of tail, i.e. measured from the mouth to the junction of trunk and tail.

The photographs were taken by Mr C. Atherton. The sections shown in Plate 4 were prepared by Mr R. Mahoney.

PLATE 1

Above : preserved specimens of *cristata* and *caroledna* of nearly equal size. The upper one is *cristata*.

Below : Details of the same individuals, shown by pinning the body walls flat and photographing the left side of setigers vii and viii, or viii and ix, at 10 times the previous magnification. In each species, one of the nephridiopores is indicated by a ruled line. The contrast between the naked nephridiopores of *cristata* and the hooded ones of *caroledna* is clearly shown. Note also the difference in size of the notopodia

PLATE 2

Dissections of specimens of *cristata* and *caroledna* of nearly equal size, to show the different proportions of the organs.

PLATE 3

Above : dissections from the dorsal side of the heads of specimens of *cristata* and *caroledna*.

Below : some of the nephridia of the left side of the two worms already shown in Plate 2. In each case, a ruled line runs to the frilly " dorsal lip " of the second nephridium, which opens on setiger vi. In *cristata* (but not in *caroledna*) the oblique muscles have been removed to expose the nephridia more clearly. The scale is the same in both pictures and the worms are of nearly equal size ; note the great difference in size of the nephrostomes.

PLATE 4

Above : transverse sections to show the relation of the nerve cord to the muscle layers of the body wall. In each picture a ruled line indicates the nerve cord. The upper four photographs show sections of setigers iii and xiv in specimens of *cristata* and *caroledna* of nearly equal size. Both of these worms were fixed in Formol-Zenker after magnesium chloride narcosis, and care has been taken to make the sections shown as comparable as possible. The other photograph shows a much smaller *caroledna*, preserved in formalin after magnesium chloride narcosis.

Below : dissection of a large *cristata*, to show that the proportions of the nehridia remain as in smaller individuals (Plates 2, 3) although the frilling of the " dorsal lip " is now more elaborate. The oblique muscle of the left side have been removed to expose the nephridia. The ruled line indicates the nephrostome of the second nephridium, as in Plate 3.

hurricanes which visited Woods Hole while the form was under investigation there in 1954, and were known to the meteorologists as Carol and Edna.

DIAGNOSES

Below are a diagnosis of the new species, and a revised one of the old. Geographical distributions cannot yet be given, for the following reason. The characters distinguishing the worms have not previously been regarded as of taxonomic importance. It is therefore impossible, in most cases, to decide from the literature whether a published record of "*A. cristata*" should be referred to *cristata* in the strict sense, to *caroledna*, or perhaps to some other form. At the present time, I am examining specimens of "*A. cristata*" from as many points as possible in the very extensive range of distribution of that supposed species, and expect to report on the results in due course.

Arenicola cristata Stimpson 1856.

Arenicola antillensis Lütken 1865.

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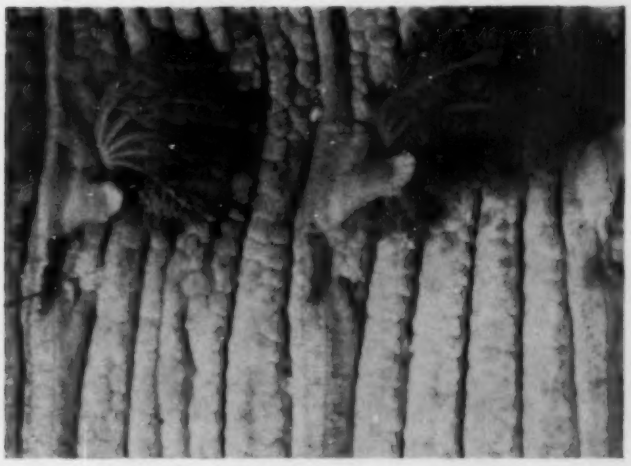
cristata 90 mm
caroledna 91 mm

50 mm in upper picture
5 mm in the others

cristata VIII

cristata IX



caroledna VII, VIII

A new lugworm from Woods Hole, Mass., U.S.A.

cristata 89 mm

caroledna 87 mm

10 mm

A new lugworm from Woods Hole, Mass., U.S.A.

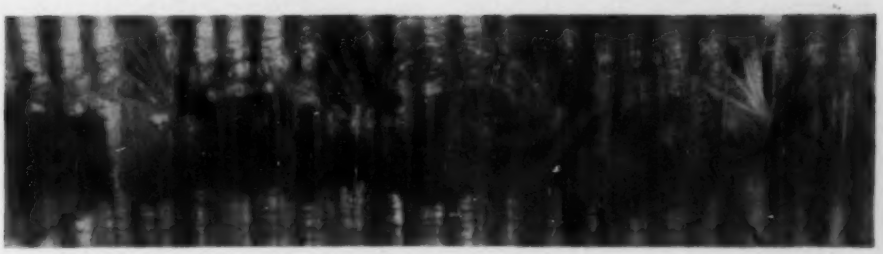
cristata 117 mm

10 mm (heads)

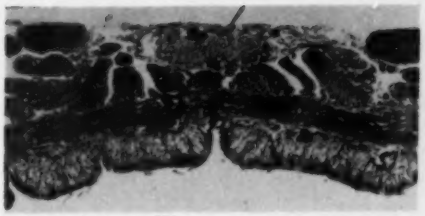
caroledna 123 mm

10 mm (nephridia)

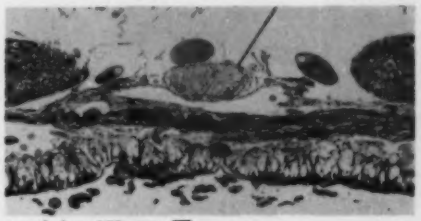
cristata 89 mm



caroledna 87 mm



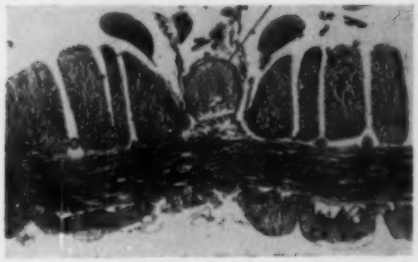
cristata, 100 mm, III.



caroledna, 107 mm, III.

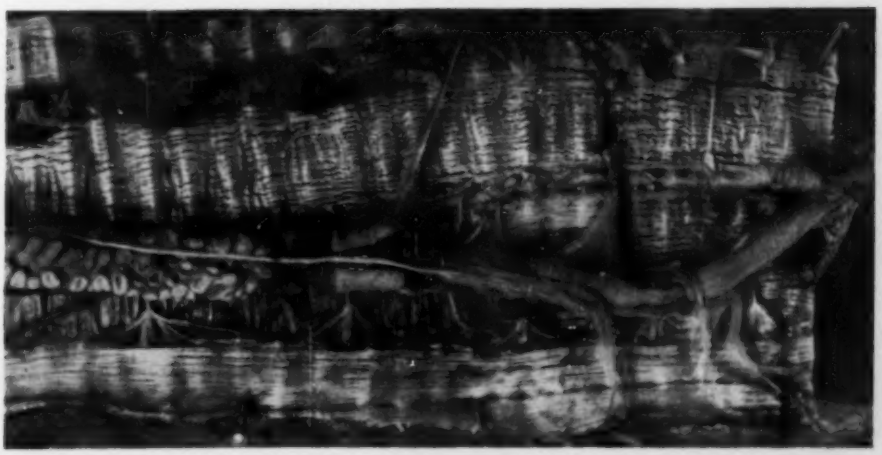
cristata, 100 mm, XIV.

0·5 mm
(all sections)



caroledna, 107 mm, XIV.

caroledna, 52 mm, XIV.



cristata 201 mm

10 mm

A new lugworm from Woods Hole, Mass., U.S.A.

STUDIES ON THE TREMATODA OF BRITISH FRESHWATER BIRDS*

BY

MARY BEVERLEY-BURTON (MRS D. F. METTRICK)

Department of Zoology and Applied Entomology, Imperial College of Science and Technology, London†

[Accepted 11th October, 1960]

(With 9 figures in the text)

The literature concerned with the helminthic fauna of Anseriformes is briefly surveyed. A host/parasite list, which includes nine new host records, the descriptions of fifteen species of trematodes which were collected from British freshwater birds during 1956–58 and a key for the separation of the genera of the subfamily Notocotylinae Kossack, 1911, are given. One other species has been described elsewhere (Beverley-Burton (1958)).

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* Part of a thesis approved by the University of London for the award of the Ph.D. degree.

† Present address: Department of Zoology, University College of Rhodesia & Nyasaland, Salisbury, S. Rhodesia.

INTRODUCTION

The present paper consists of an account of the morphology of the trematodes recovered over a period of two years (1956–58) from 209 wild birds. The majority of birds, migratory duck, were trapped at a commercial decoy at Nacton, near Ipswich, Suffolk. Others were obtained from St. James' Park, London ; Saxmundham, Suffolk ; Ascot, Berkshire and the River Thames, London.

Although helminthic parasites of domestic duck in Britain have been listed by Lewis (1930), Foggie (1933), Davies (1938), Owen (1951) and Soliman (1955), those from wild Anseriformes have been neglected. In the past many foreign authors have been reported on small collections from Anseriformes and it is only recently that any large surveys have been carried out. In America Gower (1938) autopsied 200 duck in Michigan and Schiller (1951) examined 184 birds in Alaska. In Europe Bezubik (1956) published the results of a survey of the helminths from 278 wild duck collected in Poland over a period of five years (1949–1954). Bezubik was able to collect throughout the whole year and his results indicate the seasonal fluctuations in the worm burdens of the fowl. Czaplinski (1956) described the hymenolepids (Cestoda) found in Polish Anseriformes but of the 468 birds examined some 330 were domestic fowl killed in local abattoires. As large numbers of wild duck are migratory, visiting the British Isles only during the winter months, it was decided to examine as many migrants as possible in order to ascertain what parasites are being introduced from Europe each year and also the level of infestation in each host species.

It is intended to publish an account of the Cestoda and Nematoda in future papers and also the incidence figures for each host species.

MATERIAL AND METHODS

Sixteen species of trematodes were recovered representing seven families and thirteen genera. The trematodes were fixed in cold formal-acetic under slight cover-slip pressure and were stained with Ehrlich's haematoxylin, Celestin Blue or aceto-carmine. The last gave the most satisfactory results. Sectioned material was stained with haematoxylin and eosin.

LIST OF HOSTS AND THEIR RECORDED PARASITES

(Authors' names are given with the description of each worm).

Anas platyrhynchos platyrhynchos L. (Mallard).	*Apatemon gracilis. Typhlocoelum sisowi. Echinostoma revolutum. Echinoparyphium recurvatum. Hypoderaeum conoideum. Psilochasmus oxyurus. Notocotylus attenuatus. *Notocotylus imbricatus. Catatropis verrucosa. Uniserialis gippyensis. Prosthogonimus ovatus. *Prosthogonimus cuneatus. Schistogonimus rarus. Metorchis xanthosomus.*
Anas penelope L. (Wigeon).	*A. gracilis. *T. sisowi. N. imbricatus.*
Anas crecca L. (Teal).	*A. gracilis. H. conoideum. N. imbricatus.*
Anas acuta L. (Pintail).	*T. sisowi. E. revolutum. P. oxyurus. N. imbricatus. *C. verrucosa. P. ovatus.*

Spatula clypeata (L.) (Shoveller).	*P. oxyurus. N. attenuatus. N. imbricatus. C. verrucosa. P. ovatus.*
Aythya fuligula (L.) (Tufted Duck).	*E. revolutum. E. recurvatum. *H. conoideum. *N. imbricatus.*
†*Aythya marila* (L.) (Scaup).	**Psilostomum brevicolle.*
†*Netta rufina* (Pallas) (Red-crested Pochard).	— — — —
Gallinula chloropus L. (Moorhen).	**E. revolutum. Notocotylus gibbus.*
Fulica atra L. (Coot).	— — — —
Cygnus olor (Gmelin) (Mute Swan).	— — — —
†*Gavia immer* (Brünnlich) (Common Loon).	**E. revolutum.*
†*Podiceps ruficollis* (Pallas) (Little Grebe).	— — — —

*New host record.

†Represented by single specimens.

DESCRIPTIONS OF THE SPECIES OF TREMATODES

Strigeidae Railliet, 1919

APATEMON GRACILIS (Rudolphi, 1819) Szidat, 1928

Description : Body small ; length 1·13–1·53 mm. ; length of forebody 0·38–0·61 mm., breadth 0·21–0·40 mm. ; length of hindbody 0·68–1·01 mm., breadth 0·19–0·56 mm. Ratio of measurements of forebody : hindbody 1 : 1·23 to 1 : 1·82. " Holdfast " extremely mobile in living material, may be retracted or extended beyond anterior margin of cup-shaped forebody. Oral sucker 0·09–0·14 mm. in diameter ; pharynx 0·04–0·05 mm. Oesophagus short, leading to caeca which extend to post-testicular region. Ventral sucker rounded, 0·08–0·16 mm. wide. Reproductive organs confined to hindbody. Testes bilobed, situated in tandem posterior to ovary. Anterior testis 0·14–0·19 mm. long ×0·14–0·24 mm. broad ; posterior testis 0·16–0·22 mm. ×0·11–0·26 mm. Seminal vesicle coiled between posterior testis and genital cone. Ovary spherical, 0·08–0·14 mm. in diameter. Mehlis' gland, 0·07 mm. broad, situated between testes. Uterus forming a loop anterior to ovary before passing posteriorly to genital cone. Hermaphrodite duct traversing genital cone, which projects into lumen of dorsally opening copulatory bursa. Eggs measure 101–126 microns long by 61–75 microns wide.

Hosts : *Anas p. platyrhynchos* L., *A. penelope* L., and *A. crecca* L.

Location : Intestine.

Locality : Nacton Decoy, near Ipswich, Suffolk.

Discussion : The present material agrees well with the description given by Dubois (1951) based on specimens from *Anas rubripes* and *Mareca penelope* taken in the United States. Dubois (1953) suggested that *A. gracilis* should be divided into ten subspecies. It has been observed that, in the present collection, specimens taken from the same host can be assigned to several of these subspecies. It is therefore considered preferable to regard *A. gracilis*, which is cosmopolitan with a wide host range, as a polytypic form and not as a collection of subspecies.

Cyclocoelidae Kossack, 1911

TYPHLOCOELUM SISOWI (Skrjabin, 1913) Dubois, 1959

Description : Body oval, length 5·38–8·13 mm., breadth 2·5–3·22 mm. Oral and ventral suckers apparently absent. Pharynx, with thick muscular

walls, 0·27–0·32 mm. × 0·24 mm. Intestine ring-like with 10–11 diverticula on each side. Testes oval and smooth in outline ; posterior testis measuring 0·18–0·23 mm. × 0·28–0·30 mm. ; anterior testis 0·14–0·20 mm. × 0·26–0·28 mm. Cirrus sac weakly developed, 0·28 mm. long, cirrus unarmed. Genital pore ventral to anterior margin of pharynx. Ovary transversely oval, 0·24–0·28 mm. long × 0·36–38 mm. Gonads posterior and arranged at points of an inverted triangle. Receptaculum seminis, posterior to ovary, 0·09 mm. × 0·06 mm. Transverse uterine coils filling intercaecal region. Vitellaria follicular, dorsal and lateral to intestinal caeca, extending from pharyngeal region to excretory pore. Mature eggs containing miracidia, measure 135–144 microns long by 63–74 microns wide.

Hosts : *Anas p. platyrhynchos* L., *A. penelope* L., and *A. acuta* L.

Location : Trachea and lung.

Locality : Nacton Decoy, near Ipswich, Suffolk.

Discussion : *Typhlocoelum sisowi* (Skrjabin, 1913) Dubois, 1959 is a frequently recorded parasite of anatids which, in the past, has been designated either as a synonym of *Typhlocoelum cymbium* (Diesing, 1850) or as *Tracheophilus sisowi* Skrjabin, 1913. Consequently there has been considerable confusion in the literature, e.g. Dawes (1946, 1956) adopted the former opinion, Yamaguti (1958) the latter. Dollfus (1948 a) and Dubois (1959) both give an historical account of this form and, in agreement with Dubois (1959), the designation *Typhlocoelum sisowi* is accepted.

Echinostomatidae Looss, 1902

ECHINOSTOMA REVOLUTUM (Frölich, 1802) Looss, 1899

Description : Body elongate, length 2·92–7·54 mm., breadth 0·77–1·55 mm. Cuticle spinous anteriorly, spines up to 32 microns in length. Head collar, 0·28–0·66 mm. wide, bearing 37 spines. Oral sucker 0·13–0·33 mm. long × 0·11–0·26 mm. broad, pharynx 0·16–0·32 mm. × 0·10–0·24 mm. and oesophagus up to 0·69 mm. long. Ventral sucker, 0·38–0·85 mm. long × 0·43–0·78 mm. broad, situated in anterior third of body. Gonads situated in posterior half of body. Shape of testes variable, either smooth or lobed. Anterior testis 0·20–0·57 mm. × 0·21–0·68 mm. ; posterior 0·17–0·64 mm. × 0·18–0·59 mm. Cirrus sac oval, 0·26–0·42 mm. × 0·12–0·15 mm. Ovary broader than its length 0·09–0·33 mm. × 0·16–0·54 mm. Vitellaria follicular extending from level of posterior half of ventral sucker nearly to posterior end of body. Eggs measure 96–112 microns long by 54–66 microns wide.

Hosts : *Anas p. platyrhynchos* L., *A. acuta* L., *Aythya fuligula* (L.), *Gallinula chloropus* (L.), and *Gavia immer* (Brünnlich).

Location : Intestine, intestinal caeca and cloaca.

Localities : Nacton Decoy, near Ipswich, Suffolk ; Saxmundham, Suffolk and St. James's Park, London.

As *E. revolutum* (Figs. 1 & 2) has not previously been recorded from *Gallinula chloropus or Gavia immer* a summary of the measurements of the specimens recovered from these hosts in comparison with data derived from specimens collected from *Anas platyrhynchos* and *A. acuta* is given below (Table 1).

Discussion : *Echinostoma revolutum* (Frölich, 1802) Looss, 1899 is a polytypic form which frequently occurs in Anseriformes. Beaver (1937) gave a detailed account of the morphological variability of *E. revolutum* based on a

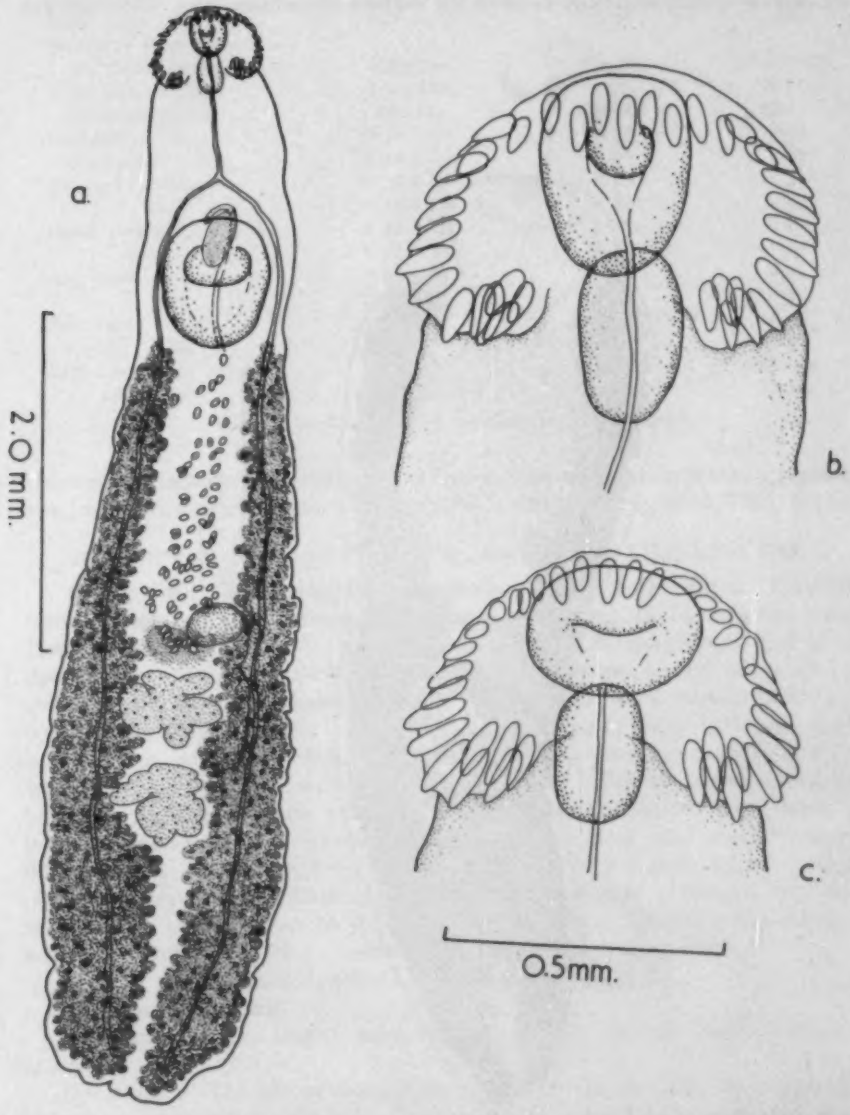

Fig. 1—*Echinostoma revolutum* (Frölich, 1802) Looss, 1899. a. Ventral view of entire specimen, from *Gavia immer* (Brünnlich) ; b. Details of head spines of the specimen depicted from *Gavia immer* ; c. Details of head spines of the specimen depicted from *Gallinula chloropus* L.

large number of specimens from a variety of hosts. Beaver correlated the relative size of several diagnostic features (e.g. the length of the lateral aboral spine of the corner group) with the body length so that specimens of various sizes can be compared. The present material agrees well with the data given by Beaver (1937) although some of the mature specimens from *Anas* spp. are

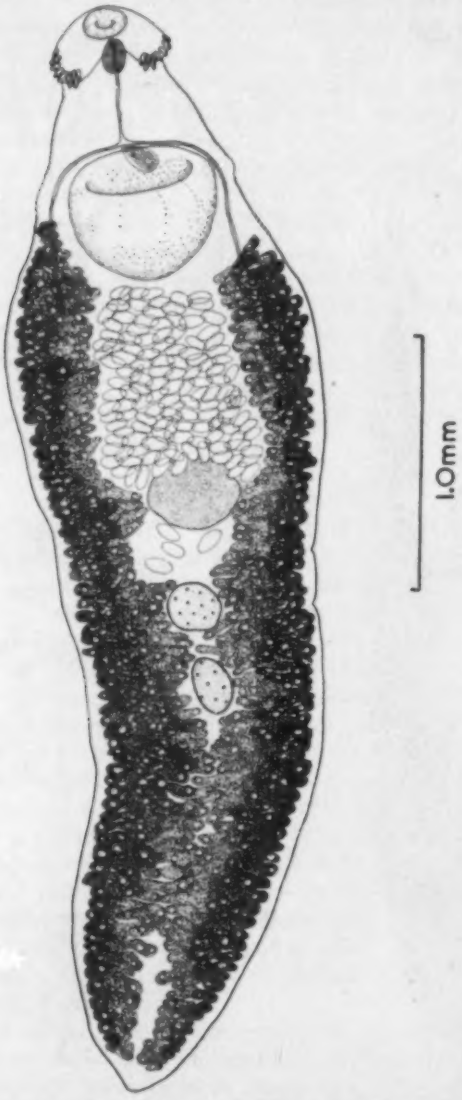

Fig. 2—*Echinostoma revolutum* (Frölich, 1802) Looss, 1899. Ventral view of entire specimen, from *Gallinula chloropus* L.

Table 1—The measurements of the organs and parts of *Echinostoma revolutum* recovered from different host species, during the present survey.

Host	*Anas platyrhynchos* *A. acuta*	*Gallinula chloropus*	*Gavia immer*
Body length	2·92–7·54	4·42	6·92
Head collar : dia.	0·28–0·64	0·46	0·66
Maximum dimensions of :—			
(a) Corner spines	112×50μ	85×38μ	102×42μ
(b) Lateral spines	101×42μ	77×32μ	95×35μ
(c) Dorsal spines	98×42μ	74×32μ	92×35μ
Oral sucker : dia.	0·11–0·26	0·22	0·26
Ventral sucker : dia.	0·43–0·78	0·63	0·70
Pharynx : length	0·16–0·28	0·23	0·32
dia.	0·10–0·24	0·12	0·19
Ovary : length.	0·09–0·33	0·25	0·32
dia.	0·16–0·48	0·37	0·54
Ant. testis : length	0·30–0·57	0·20	0·40
dia.	0·25–0·68	0·21	0·66
Post. testis : length.	0·17–0·64	0·25	0·52
dia.	0·28–0·59	0·19	0·54
Eggs : length.	103–112μ	100–108μ	96–98μ
dia.	56–66μ	58–62μ	54–58μ

Unless otherwise stated all measurements are in mm.

considerably smaller than average. (This species may attain a much greater size, up to 22 mm. in length and 3 mm. in breadth (Dawes, 1946, 1956) Ed.).

ECHINOPARYPHIUM RECURVATUM (von Linstow, 1873) Lühe, 1909

Description : Body elongate and slender, length 3·29–4·7 mm., breadth 0·58–0·74 mm. Cuticle armed with spines measuring 14–16 microns long. Head collar, 0·30–0·42 mm. in diameter, bears 43–45 spines arranged in a double row. Corner spines 61–72 microns long ; spines of oral series 53–57 microns and those of aboral series 56–68 microns. Oral sucker globular, 0·09–0·14 mm. in diameter ; pharynx 0·09–0·14 mm. long, 0·08–0·12 mm. broad ; oesophagus up to 0·75 mm. long. Ventral sucker in anterior third of body, length 0·35–0·46 mm., breadth 0·31–0·42 mm. Testes smooth and oval in shape ; anterior testis 0·30–0·47 mm. long and 0·19–0·27 mm. broad ; posterior testis 0·33–0·47 mm.×0·19–0·24 mm. Cirrus sac oval, length 0·28–0·38 mm. breadth 0·16–0·21 mm. ; cirrus up to 0·47 mm. long. Ovary rounded, length 0·11–0·18 mm., breadth 0·12–0·17 mm. Vitelline follicles transversely oval and up to 0·14 mm. in diameter. Eggs few (maximum number 31) measuring 98–113 microns long by 66–75 microns wide.

Hosts : *Anas p. platyrhynchos* L. and *Aythya fuligula* (L.).

Location : Intestine.

Locality : Nacton Decoy, near Ipswich, Suffolk and St. James's Park, London.

Discussion : The above description applies to the material from *Aythya fuligula* which was fully mature. The specimens from *Anas p. platyrhynchos* (some of which had 43 head spines) were small and immature with few or no eggs in the uterus.

The specimens of *E. recurvatum* recovered during the present survey are very like those described by Dietz (1910) and Skrjabin (1956). Yamaguti (1939) proposed a subspecies, *E. recurvatum vanelli* from *Vanellus vanellus*, on the basis that in just over 25 per cent of his specimens (in fact nine out of thirty-two) the vitelline follicles extend anteriorly to the level of the posterior border of the ventral sucker. Yamaguti did not give the sizes of the oral and aboral spines separately although he stated that there is a difference in size. According to Skrjabin (1956), Oschmarin in 1956 described another subspecies, *E. recurvatum cerci* from *Cercus melanoleucus* based on a single specimen. The measurements given by Oschmarin for this form closely resemble the data obtained from immature material in the present collection. According to Yamaguti (1958) a third subspecies, *E. recurvatum indianum* was suggested by Verma, 1936 for specimens taken from common snipe and brahmany duck in India.

As there appears to be some variation in the size of *E. recurvatum* from different collections it is questionable if the subspecies mentioned above are valid.

HYPODERAEUM CONOIDEUM (Bloch, 1782) Dietz, 1909

Description : Body elongate, length 6·87–8·74 mm., breath at level of ventral sucker 0·80–1·09 mm. Cuticle spinous anteriorly, spines up to 16 microns long. Head collar small, 0·35–0·47 mm. in diameter, bearing 47–49 spines. Corner spines measure 25–27 microns long by 11 microns broad ; marginal spines 20–23 microns by 9 microns. Oral sucker 0·19–0·24 mm. long and 0·18–0·25 mm. broad ; pharynx 0·14–0·20 mm. × 0·10–0·14 mm. ; oesophagus 0·05–0·09 mm. long. Ventral sucker in anterior fifth of body 0·66–0·78 mm. long and 0·55–0·80 mm. broad. Testes and ovary situated in middle third of body. Testes elongate and irregular in outline ; anterior testis 0·59–0·91 mm. long and 0·16–0·51 mm. broad ; posterior testis 0·56–0·90 mm. × 0·14–0·57 mm. Cirrus sac variable in size and shape, maximum length 0·98 mm. Ovary transversely oval 0·18–0·28 mm. long and 0·21–0·31 mm. broad. Uterus forming irregular coils anterior to ovary. Metraterm conspicuous, having thickened walls, 0·06 mm. in diameter. Vitellaria in two bands extending from level of posterior margin of ventral sucker to posterior end of body. Eggs 94–112 microns long by 56–65 microns broad.

Host : *Anas p. platyrhynchos* L., *A. crecca* L. and *Aythya fuligula* (L.).

Location : Intestine and rectum.

Locality : Nacton Decoy, near Ipswich, Suffolk.

Discussion : According to Skrjabin (1956) of seven species assigned to the genus *Hypoderaeum* five have a similar number of head spines. They are :— *H. conoideum* with 47–53 spines ; *H. gnedini* Baschkirova, 1941 with 51 spines ; *H. vigi* Baschkirova, 1941 with 43 spines ; *H. skrjabini* Oschmarin, 1946 with 49 spines and *H. microspina* (Singh, 1954) with 47 spines. One of the most detailed descriptions of *H. conoideum* is that of Rees (1932) whose specimens carried 43–45 spines so that the range for *H. conoideum* should probably be extended from 45–53 as quoted by Skrjabin (1956) to 43–53 spines.

If the measurements of the above five species are compared (Table 2) it will be seen that there is considerable overlapping. It is suggested that the validity of *H. gnedini*, and *H. skrjabini* is questionable as they are very similar to *H. conoideum*. An examination of the type specimens of these forms would possibly result in their being synonymised with *H. conoideum*. Yamaguti (1958) has used the designation *Echinostoma microspina* Sing, 1954 ignoring the transfer of this species to the genus *Hypoderaeum* by Skrjabin and Baschkirova in 1956 which was included by Skrjabin (1956). Yamaguti (1958) placed *H. skrjabini* in the genus *Echinochasmus* although, from the figure given in Skrjabin (1956) of this species, there is no evidence of a break in the dorsal row of head spines which is a diagnostic feature of the genus *Echinochasmus*. The head spines of *H. vigi* are larger than those of the other species included above so that it is easily separated from *H. conoideum*.

Table 2—The measurements of the various species of *Hypoderaeum* described with 43–53 head spines. Unless otherwise stated all measurements are in mm.

	H. gnedini Baschkirova 1941	*H. microspina* (Singh, 1954)	*H. conoideum* (after Rees 1932)	*H. skrjabini* Oschmarin, 1947	*H. vigi* Baschkirova, 1941
Body l.	5·4–7·52	7·84	8·2–10·2	11	12·8
Body b.	1·0–1·36	0·87	0·87	2·5	2·2
Number of Head-spines	51	47	43–45	49	43
Size of spines	22×16μ	20·7μ	25×10μ	29×13μ	51–66μ · ×12–17μ
Corner spines l.	—	25μ	—	39×13μ	
Collar dia.	0·32–0·37	0·39	0·5–0·6	0·22(?)	0·56
O. Sucker dia.	0·18	0·19	0·21	0·22	0·20
V. Sucker dia.	0·64–1·0	0·70	0·98	1·17	1·20
Phar. dia.	0·17	0·11	0·15	0·11	0·23
Ant. testis l.	0·56–1·04	0·72	0·98	0·23	1·48
Post. testis l.	0·62–1·00	0·80	0·90	1·02	1·48
Ovary l.	0·28–0·30	—	0·14	0·31	0·44
Ovary b.	0·28–0·39	0·26	0·26	0·66	0·61
Vit. foll. dia.	—	0·04	0·05–0·1	—	—
Eggs l.	99–110μ	85–92μ	60–110μ	105μ	86–108μ
Eggs b.	66μ	46–53μ	60–90μ	66μ	56–65μ
Cirrus sac. l.	0·44–0·66	0·3	—	0·94	1·02
Cirrus sac. b.	0·17–0·39	0·2	—	0·35	0·56

Psilostomatidae Odhner, 1913

PSILOSTOMUM BREVICOLLE (Creplin, 1829) Braun, 1902

Description : Body, length 2·96–3·08 mm., breadth 0·70–0·93 mm. Cuticle apparently unarmed. Oral sucker conspicuous, 0·28–0·30 mm. long by 0·31–0·35 mm. in breadth ; pharynx almost square in outline with a large lumen 0·18–0·21 mm. × 0·19 mm. ; oesophagus short and epithelial, up to 0·06 mm. long. Ventral sucker slightly smaller than oral sucker, 0·25 mm. × 0·24–0·27 mm. Testes smooth or irregular in outline situated in posterior half of body. Anterior testis 0·24–0·39 mm. long and 0·24–0·26 mm. broad ; posterior testis 0·37–0·38 mm. × 0·19–0·26 mm. Cirrus sac elongate and slender, 0·66–0·75 mm. long and 0·08 mm. in breadth at base, curving round ventral

sucker. Cirrus unarmed. Ovary transversely oval, 0·08–0·09 mm. long by 0·11 mm. broad, situated just inside posterior half of body in front of testes. Vitelline follicles oval, up to 0·10 mm. in diameter, confined to posterior two-thirds of body. Eggs few (up to 30 in number) measure 106–113 microns long by 50–56 microns wide.

Host : *Aythya marila* (L.).

Location : Intestine.

Locality : River Thames, London.

Discussion : Price (1942) listed five species in the genus *Psilostomum*. Skrjabin (1947) recognised nine species, while Mettrick (1956) considered that *P. brevicolle* (Creplin, 1829) and *P. cygnei* Southwell and Kirschner, 1937 were the only species that could be included. Yamaguti (1958) retained *P. platyurum* (Mühling, 1898) as type species of the genus *Psilostomum* although Braun (1902) declared *platyurum* to be a synonym of *brevicolle*. Yamaguti (1958) recognised the following species :— *P. brevicolle* (Creplin, 1829), *P. cygnei* Southwell & Kirschner, 1937, *P. lineatum* Linton, 1928, *P. marliae* Price, 1942 and *P. progeneticum* Wisniewski, 1932. Yamaguti considered *P. plicatum* Linton to be in the genus *Bianum* while *P. varium* was transferred to a new genus *Pseudopsilostoma*.

The description given by Lühe (1909) of *P. brevicolle* agrees well with that of the present material.

PSILOCHASMUS OXYURUS (Creplin, 1825) Lühe, 1909

Description : Body, length 2·54–3·34 mm., breadth 0·62–1·08 mm., in the region of the testes, tapering towards anterior and posterior extremities ; the latter having a partly retractile " tail ". Oral sucker oval, 0·24–0·31 mm. long and 0·16–0·22 mm. broad ; pharynx 0·10–0·14 mm. × 0·07–0·12 mm. ; oesophagus epithelial, up to 0·47 mm. long. Caeca extending almost to posterior end of body. Ventral sucker, 0·33–0·39 mm. in diameter, situated in middle third of body. Testes irregular in outline and located in posterior half of body. Anterior testis 0·15–0·36 mm. long and 0·19–0·38 mm. broad ; posterior testis 0·19–0·47 mm. × 0·16–0·36 mm. Cirrus sac elongate and slender, 0·75–0·97 mm. × 0·08–0·11 mm. extending from level of ovary to genital pore. Cirrus non-spinous, up to 0·8 mm. long. Ovary transversely oval, 0·09–0·14 mm. × 0·11–0·16 mm. and situated slightly to left of mid-line. Vitelline follicles extending from just behind ventral sucker to attenuated region at posterior end of body. Uterus having a small fold posterior to ovary, ascending uterus contains few eggs (up to 33 in number). Eggs measure 100–112 microns by 56–57 microns.

Hosts : *Anas p. platyrhynchos* L., *A. acuta* L. and *Spatula clypeata* (L.).

Location : Anterior region of intestine.

Locality : Nacton Decoy, near Ipswich, Suffolk.

Discussion : Lühe (1909) erected the genus *Psilochasmus* designating *Distoma oxyurum* Creplin, 1825 as genotype. A second species, *longicirratus*, was added by Skrjabin (1913) for specimens with a long cirrus sac. Braun (1902) had described the cirrus sac in *oxyurus* as long and slender and Odhner (1913) stated that the base of the cirrus sac in *oxyurus* was situated just in

front of the ovary. Both these descriptions could be applied to *P. longicirratus* as well as *P. oxyurus*.

Stunkard & Dunihue (1931) assigned specimens from a Long Island duck to *P. oxyurus* and regarded *P. longicirratus* as a synonym of the genotype as the only feature separating the two forms was the difference in the length of the cirrus sac ; an extremely variable character. Subsequently, Tabangui (1932) and Cannon (1938) considered *P. longicirratus* as a valid species while, among others, Gower (1938) and Singh (1954) used the name *P. oxyurus* which is now becoming generally accepted. Yamaguti (1958) regarded *P. oxyurus* as genotype and also accepted *P. longicirratus* as a valid species.

Other species which have been placed in the genus *Psilochasmus* are : *P. agilis* Travassos, 1925, *P. japonicus* Ishii, 1935 and *P. skrjabini* Gnedina, 1946. From the description given by Ishii (1935) it is suggested that *P. japonicus* is a synonym of *P. oxyurus*.

Notocotylidae Lühe, 1909

NOTOCOTYLUS ATTENUATUS (Rudolphi, 1809) Kossack, 1911

Description : Body, length 2·01–2·96 mm. breadth 0·48–0·83 mm. Cuticle spinous ventrally. As is usual in the genus *Notocotylus*, the ventral glands are arranged in three longitudinal rows ; median row with 14–15 glands ; lateral rows with 16–17 glands each ; most usual combination 17/15/17 (Fig. 3). Anterior gland of median row lies between 20–24/100 body length and $\frac{1}{2}$ or $1\frac{1}{2}$ intervals in front of anterior glands of lateral rows. The latter lie between 22–27/100 body length. Oral sucker 0·10–0·17 mm. long and 0·10–0·22 mm. broad ; pharynx absent ; oesophagus up to 0·17 mm. long. Testes posterior and extracaecal in position. Right testis 0·27–0·47 mm. long and 0·14–0·33 mm. broad ; left testis 0·28–0·42 mm. × 0·11–0·33 mm. Outer margins of testes lobed ; inner margins with less pronounced lobation. External seminal vesicle situated dorsal to uterine coils ; distal portion of vesicle lies in longitudinal axis of body, while proximal region is coiled near base of cirrus sac. Cirrus sac elongate, 0·75–0·94 mm. × 0·06–0·09 mm. in maximum breadth, containing an internal seminal vesicle and a long ejaculatory duct. Base of cirrus sac situated just inside anterior half of body. Cirrus bearing small spines. Ovary 0·11–0·34 mm. long and 0·11–0·32 mm. broad, irregular in outline and situated between testes. Mehlis' gland, 0·04–0·26 mm. long and 0·11–0·24 mm. broad, situated just in front of ovary. Receptaculum seminis absent. Uterus with ascending limb only, forming a series of transverse intercaecal coils. Total number of uterine coils 10–19 ; number anterior to vitellaria 4–6. Metraterm 0·47–0·66 mm. × 0·05–0·06 mm. Ratio of measurements of cirrus sac and metraterm 1 : 0·55 to 1 : 0·70 (Fig. 4). Common genital pore situated just behind bifurcation of gut and 0·18–0·30 mm. from anterior margin of body. Vitelline follicles irregular, arranged in 2 narrow extra-caecal bands, confined to posterior half of body. Vitelline ducts pass between testes and posterior uterine slings to meet in middle line, dorsal to Mehlis' gland. Excretory canals (2) extending from oesophageal region to small excretory vesicle which opens by dorsal excretory pore, midway between

ovary and posterior margin of body. Eggs 19–20 microns long by 11–13 microns wide bear long polar filaments.

Hosts : *Anas p. platyrhynchos* L., and *Spatula clypeata* (L.).

Location : Intestinal caeca.

Locality : Nacton Decoy, near Ipswich, Suffolk.

Discussion : *Monostomum attenuatum* was first described by Rudolphi in 1809. Diesing (1839) erected the genus *Notocotylus* designating *triserialis* Diesing, 1839 as genotype. Kossack (1911) considered that *triserialis* was

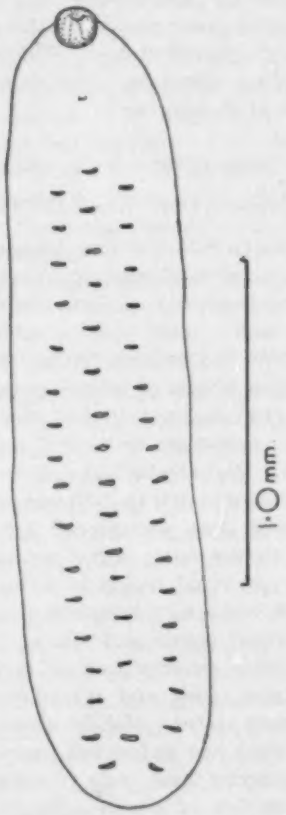

Fig. 3—*Notocotylus attenuatus* (Rudolphi, 1809) Kossack, 1911. Entire specimen, ventral view to show the pattern of the ventral glands.

synonymous with *attenuatus* and proposed the combination *Notocotylus attenuatus*. This designation had been used ever since. Dubois (1951), who gave a detailed historical review of the genus *Notocotylus*, concluded that *N. attenuatus* should be regarded as "species inquirendae" and that *N. triserialis* should be revived as genotype.

The designation *N. attenuatus* (Rudolphi, 1809) Kossack, 1911 has been in use for nearly fifty years and it is impossible to prove or disprove Kossack's opinion that *trisérialis* is synonymous with *attenuatus*. The type material of the latter, according to Dubois (1951), having been destroyed. It is suggested

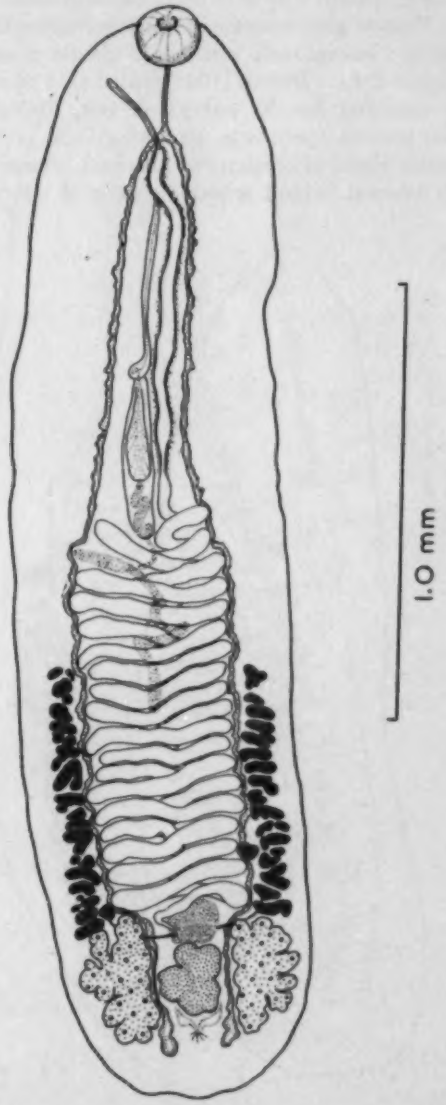

Fig. 4—*Notocotylus attenuatus* (Rudolphi, 1809) Kossack, 1911. Entire specimen, ventral view to show the internal anatomy.

therefore that no useful purpose is to be gained by reviving disused names to replace widely accepted designations of long standing and that the name *Notocotylus attenuatus* should be retained.

NOTOCOTYLUS IMBRICATUS (Looss, 1893) Szidat, 1935

Description : Body, length 2·31–4·73 mm., breadth 0·63–1·46 mm. Cuticle spinous ventrally. Ventral glands arranged in three longitudinal rows ; median row with 14–15 glands ; lateral rows with 16–17 glands in each, total number of glands 46–49, (Figs. 5 & 6). Dubois (1951) stated that 46 was the maximum number of glands recorded for *N. imbricatus* but, Dubois confirmed the identification of the present specimens with 49 glands (1958—private communication). Anterior gland of median row situated between 14–17/100 body length and half an interval behind anterior glands of lateral rows which lie

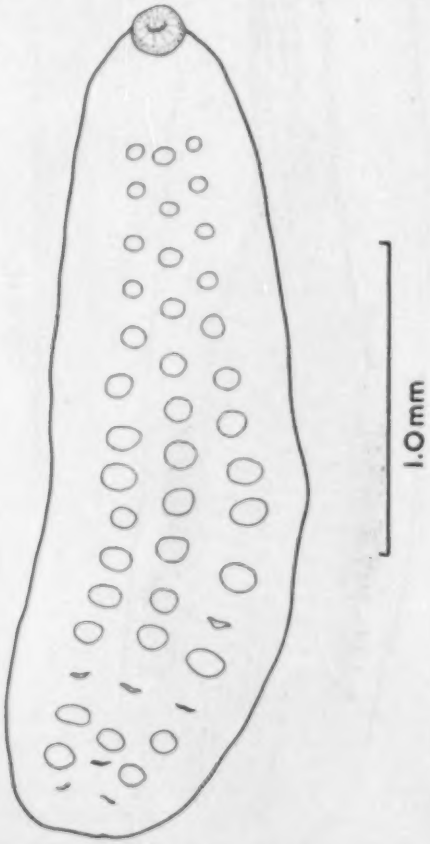

Fig. 5—*Notocotylus imbricatus* (Looss, 1893) Szidat, 1935. Entire specimen, ventral view to show the pattern of the 46 ventral glands.

between 12–16/100 body length (see Table 3). Oral sucker transversely oval, 0·10–0·17 mm. × 0·11–0·22 mm. ; pharynx absent ; oesophagus up to 0·17 mm. long. Testes posterior and extracaecal in position. Right testis 0·31–0·71 mm. long and 0·14–0·33 mm. broad ; left testis 0·28–0·71 mm. × 0·16–0·33 mm. Outer margins of testes having three to five primary lobes which may be sub-

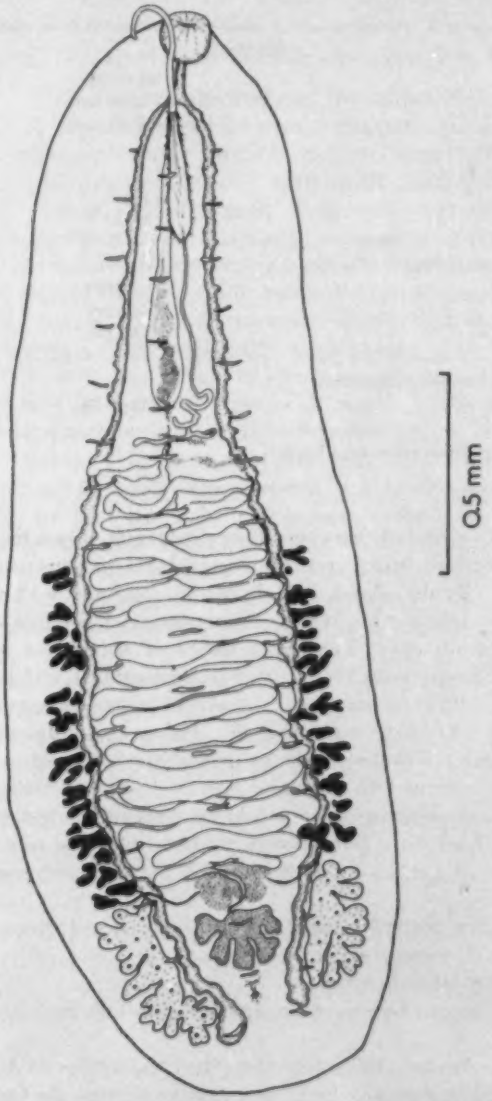

Fig. 6—*Notocotylus imbricatus* (Looss, 1893) Szidat, 1935. Entire specimen, ventral view to show the internal anatomy and the pattern of the 49 ventral glands.

divided ; inner margins less markedly lobed. External seminal vesicle dorsal to uterine coils, its distal portion situated in the sagittal plane ; proximal portion coiled in front of transverse uterine folds. Cirrus sac elongate, 0·61–0·15 mm. × 0·06–0·09 mm., containing internal vesicle and ejaculatory duct. Base of cirrus sac situated in anterior half of body. Cirrus bearing small spines.

Table 3—Data concerning *N. attenuatus* and *N. imbricatus* (compiled from material in the present collection).

	N. attenuatus.	*N. imbricatus.*
Length of body.	2·01–2·96 mm.	2·31–4·73 mm.
Breadth of body.	0·48–0·83 mm.	0·63–1·46 mm.
No. of ventral glands in :—		
Median row.	14–15	14–15
Lateral rows.	16–17	16–17
Situation in relation to length of body :—		
1st. med. gland.	20–24/100	14–17/100
1st. lat. gland.	22–27/100	12–16/100
Base of cirrus sac.	41–50/100	35–43/100
Ratio of measurements of metraterm : cirrus sac.	0·55–0·70	0·41–0·47
Posn. of 1st. med. gland in relation to 1st. lat. gland.	$+\frac{1}{2}$, $+1\frac{1}{2}$.	$-\frac{1}{2}$.

Ovary posterior, situated between testes. Ovary measures 0·11–0·34 mm. long and 0·15–0·32 mm. broad ; posterior and lateral margins usually indented to form five lobes. Mehlis' gland, 0·08–0·26 mm. long and 0·12–0·36 mm. broad, lies immediately anterior to ovary. Receptaculum seminis absent. Uterus with ascending limb only, forming a series of transverse intercaecal coils. Total number of uterine coils 17–20 ; 2–9 coils anterior to vitellaria. Metraterm 0·28–0·44 mm. × 0·03–0·05 mm. wide. Ratio of measurements of cirrus sac and metraterm is 1 : 0·41 to 1 : 0·47 (Fig. 6). Common genital pore, just behind bifurcation of gut. Vitelline follicles irregularly arranged in two narrow extracaecal bands, confined to posterior half of body. Vitelline ducts passing between testes and posterior uterine fold to meet in sagittal plane ; dorsal to Mehlis' gland. Excretory pore dorsal, midway between ovary and posterior margin of body. Eggs, 18–22 microns long by 10–12 microns wide, bear long polar filaments.

Hosts : *Anas p. platyrhynchos* L., *A. penelope* (L.), *A. crecca* L., *A. acuta* L., *Spatula clypeata* (L.) and *Aythya fuligula* (L.).

Location : Intestinal caeca.

Locality : Nacton Decoy, near Ipswich, Suffolk and St. James's Park, London.

Discussion : Szidat (1935) first described the adults of *N. imbricatus* that were obtained experimentally by feeding *Cercaria imbricata* Looss to ducklings. Szidat separated *imbricatus* from *attenuatus* on differences in the pattern of the ventral glands and (1936) listed nine species of *Notocotylus*, retaining

N. imbricatus as a separate form. This was accepted by Harwood (1939) and by Dubois (1951) although *imbricatus* has often been regarded as a synonym of *attenuatus*. It is suggested that several descriptions of *N. attenuatus* based on collections of adult material may have been a mixture of these two species which are, in the present work, recognised as distinct forms.

NOTOCOTYLUS GIBBUS (Mehlis, 1846) Kossack, 1911

Description : Body, length 1·06–2·90 mm., breadth 0·69–1·36 mm. Ventral glands arranged in three longitudinal rows ; median row with 4–5 glands ; lateral rows with 11 glands in each. In uncleared specimens ventral glands appear as clusters of cream coloured follicles with small inconspicuous transverse apertures. Oral sucker 0·10–0·19 mm. long and 0·11–0·21 mm. broad ; oesophagus 0·05–0·11 mm. long ; pharynx absent. Testes extracaecal, posterior in position and irregularly oval in outline. Right testis 0·14–0·52 mm. long and 0·13–0·28 mm. broad ; left testis 0·14–0·40 mm. × 0·14–0·30 mm. External seminal vesicle dorsal to uterus ; distal limb in sagittal plane, proximal region having a single coil to right of cirrus sac. Cirrus sac prominent, 0·30–0·75 mm × 0·07–0·20 mm. Base of cirrus sac situated in middle third of body. Cirrus having spines 9–11 microns in length. Ovary 0·11–0·31 mm. long and 0·11–0·28 mm. broad, rounded or irregularly oval in shape, situated between testes. Mehlis' gland 0·09–0·14 mm. long and 0·24–0·28 mm. broad. Uterus having ascending limb only, forming 6–9 transverse folds of which 3–5 are anterior to the vitellaria. Metraterm thick-walled, conspicuous, 0·19–0·46 mm. long and 0·05–0·09 mm. broad. Vitelline follicles irregularly arranged in two extracaecal bands which extend from midbody to level of testes. Excretory pore dorsal, midway between ovary and posterior margin of body. Eggs, 19–20 microns long by 9–11 microns wide, bearing long polar filaments.

Hosts : *Gallinula chloropus* (L.).

Location : Intestinal caeca.

Locality : Great Glemham, Saxmundham, Suffolk.

The historical aspect of *Notocotylus gibbus* has been discussed by Dubois (1951).

Lal (1935) erected the genus *Hindia*, with *N. gibbus* (Mehlis, 1846) as type, for species of the genus *Notocotylus* in which the genital pore was situated " at the intestinal fork ". Szidat (1936) proposed the genus *Kossackia* for species of *Notocotylus* with three rows of non-evaginable ventral glands and designated *gibbus* as type. Harwood (1939) invalidated both *Hindia* and *Kossackia* although it was suggested that *N. gibbus*, *N. pacifera* (Noble, 1933) *N. regis* Harwood, 1939 and *N. porzanae* Harwood, 1939 formed a natural group with the following characters :— relatively short body ; ventral glands flat and not absolutely protrusable ; parasitic in the intestinal caeca of Rails. Harwood commented that other species of the genus *Notocotylus* have these characters e.g. *N. ralli* Bayis, 1928 occurs in *Rallus aquaticus* but has a gland pattern that suggests the " *attenuatus* group " while *N. filamentis* Barker, 1915 with relatively non-protrusable glands has a relatively long body and is parasitic in musk rats.

Dubois (1951) suggested that the "*gibbus* group" listed by Harwood (1939) should be assigned to the subgenus *Hindia* Lal, 1935 with *N. gibbus* (syn. *N. pacifera* (Noble, 1933)) as type and *N. porzanae* Harwood, 1939 as "forme consubgénérique". According to Dubois, species of *Notocotylus* assigned to the subgenus *Hindia* have the following characters :— body relatively short and oval ; four to six weakly protrusable ventral glands in the median row ; cuticle unarmed ; parasitic Rails. *N. regis* Harwood, 1939 which is parasitic in Rails was included in the "*gibbus* group" by Harwood (1939) has ten ventral glands in the median row and is thus, according to Dubois (1951), excluded from the subfamily *Hindia*. A similar anomaly is *N. skrjabini* described by Ablassov in Skrjabin (1953). *N. skrjabini* has five ventral glands in each of three rows and the body is oval in shape. Thus *N. skrjabini* is eligible for inclusion in the subgenus *Hindia* but the ventral glands are evaginable and the type material was recovered from *Anas platyrhynchos*.

From the above examples it is clear that there is not, as yet, sufficient evidence to support the erection of a subgenus to accommodate the "*gibbus* group" of the genus *Notocotylus*. It is suggested that the subgenus *Hindia* Lal, 1953 which is accepted by Dubois (1951) should not be recognised.

CATATROPIS VERRUCOSA (Frölich, 1789) Odhner, 1905

Description : Body, length 3·74–4·24 mm., breadth 1·10–1·18 mm. Cuticle armed with spines on ventral surface. Ventral keel extends from level of base of cirrus sac to posterior margin of ovary. Two rows of ventral glands lie on either side of ventral keel ; 8–10 glands in each row. Oral sucker 0·19–0·21 mm. long and 0·21 mm. broad ; pharynx and ventral sucker absent. Testes posterior and extracaecal, lobed on outer margins. Right testis 0·61–0·68 mm. long and 0·33–0·37 mm. broad ; left testis 0·66–0·71 mm. × 0·28–0·38 mm. External seminal vesicle having two to three loops anterior to uterine coils. Cirrus sac, 1·32–1·50 mm. × 0·19–0·24 mm., containing internal seminal vesicle and ejaculatory duct. Cirrus armed with small spines. Ovary, 0·31–0·39 mm. long and 0·27–0·30 mm. broad, irregular in outline and situated posteriorly between testes. Mehlis' gland immediately anterior to ovary, length 0·19–0·24 mm., breadth 0·28 mm. Uterus with ascending limb only, with 17–20 transverse coils of which 3–4 are anterior to vitellaria. Metraterm 0·94–1·03 mm. × 0·05–0·08 mm. Ratio of measurements of cirrus sac and metraterm 1 : 0·63 to 1 : 0·78. Metraterm and cirrus sac open at genital pore just behind bifurcation of gut. Vitelline follicles extend from middle of body to anterior margin of testes as two extracaecal bands. Eggs measure 20 microns long by 14 microns wide and carry long polar filaments.

Hosts : *Anas p. platyrhynchos* L., *A. acuta* L., and *Spatula clypeata* (L.).

Location : Intestinal caeca.

Locality : Nacton Decoy, near Ipswich, Suffolk.

Discussion : *Catatropis verrucosa* has been recorded and described frequently from Anseriformes. The writer's specimens agree well with the description given by Odhner (1905) who erected the genus *Catatropis* for notocotylids with a midventral keel flanked by two rows of glands.

UNISERIALIS GIPPYENSIS Beverley-Burton, 1958

Description : This material has been described previously (Beverley-Burton, 1958).

Host : *Anas p. platyrhynchos* L.

Location : Intestinal caeca and bursa Fabricii.

Locality : Nacton Decoy, near Ipswich, Suffolk.

Discussion : The original description of *U. gippyensis* Beverley-Burton, 1958 was based on material recovered from three mallards taken at Nacton Decoy in 1956 and 1957. Subsequently, in 1958, another fifteen specimens of *U. gippyensis* were found in a mallard at Nacton.

A KEY FOR THE SEPARATION OF THE GENERA OF THE SUBFAMILY NOTOCOTYLINAE KOSSACK, 1911. (Based on that of Harwood (1939))

1. Posteriorly the vitellaria extend some distance beyond the anterior borders of the testes.....*Hofmanostomum* Harwood, 1939.
   Posteriorly the vitellaria extend only as far as, or slightly beyond, the anterior borders of the testes..... 2
2. Ventral glands absent..... 3
   Ventral glands arranged in one to five rows..... 4
3. Three ventral ridges present.....*Tristriata* Belopolskaia, 1953.
   Ventral ridges absent.....*Paramonostomum* Lühe, 1909.
4. Two lateral rows of ventral glands, median row represented by a glandular ridge .....*Catatropis* Odhner, 1905.
   Either one, three or five rows of ventral glands, median row represented by discrete glandular patches..... 5
5. One row of ventral glands, cirrus unarmed .....*Uniserialis* Beverley-Burton, 1958.
   More than one row of ventral glands..... 6
6. Three rows of ventral glands, cirrus armed or unarmed.....*Notocotylus* Diesing, 1839.
   Five rows of ventral glands, cirrus armed with heavy spines.....*Quinqueserialis* Skvorozov, 1934.

Prosthogonimidae Lahille, 1922

PROSTHOGONIMUS OVATUS (Rudolphi, 1803) Lühe, 1899

Description : Body pyriform, length 2·12–3·27 mm., breadth 1·15–1·98 mm. Cuticle spinous anteriorly. Oral sucker terminal, length 0·19–0·25 mm. breadth 0·17–0·23 mm. Prepharynx short, pharynx 0·07–0·14 mm. × 0·09–0·13 mm., oesophagus up to 0·35 mm. long. Ventral sucker 0·24–0·36 mm. long and 0·23–0·36 mm. broad, situated in anterior half of body. Testes lobed, lying side by side in posterior half of body. Right testis 0·25–0·38 mm. long by 0·13–0·25 mm. broad, left testis 0·23–0·30 mm. × 0·12–0·24 mm. Cirrus sac sinuous, 0·56–0·66 mm. × 0·09 mm., extending from level of bifurcation of gut to common genital pore, which is anterior and left of oral sucker. Cirrus apparently non-spinous. Ovary follicular, almost completely dorsal to ventral sucker, length 0·21–0·30 mm., breadth 0·24–0·39 mm. Mehlis' gland diffuse, posterior to ovary. Receptaculum seminis measures 0·05–0·07 mm. × 0·05–0·09 mm. Uterus having folded, descending and ascending limbs, uterine coils mainly intercaecal in posterior part of body, extending over caecum on left

side in front of ventral sucker. Metraterm thin-walled. Vitellaria mainly extracaecal, extending from anterior margin of ventral sucker to posterior margin of testes, the follicles arranged either in a continuous band or in clusters. Excretory pore dorsal, posterior margin of body, vesicle Y-shaped, lateral ducts uniting in testicular region. Eggs measure 25–32 microns long by 14–16 microns in diameter.

Hosts : *Anas p. platyrhynchos* L., *A. acuta* L., and *Spatula clypeata* (L.).

Location : Bursa Fabricii.

Locality : Nacton Decoy, near Ipswich, Suffolk.

Discussion : The genus *Prosthogonimus* has been reviewed by several authors e.g., Tseng (1932), Macy (1934), Witenberg and Eckmann (1939), Chauhan (1940), Ku (1940), Dollfus (1948), and Chen (1951). Most of these papers have included keys to separate the numerous species of *Prosthogonimus* that have been described.

It is unfortunate that differences in the relative sizes of the oral and the ventral suckers have often been used for the separation of species within the genus. Lühe (1909), Skrjabin (1913), Tseng (1932) and Macy (1934) all used this feature and the latter specified that *P. ovatus* should fall into the group in which the " ventral sucker is at least half larger than the oral sucker ". In the present material this feature is most unreliable. In four specimens from *Spatula clypeata* the ratios of the diameters of the oral : ventral suckers are :— 1 : 1·39, 1 : 1·39, 1 : 1·25 and 1 : 1·20 ; in a single specimen from *Anas platyrhynchos* the ratio is 1 : 1·58 and in another specimen from *A. acuta* the ratio is 1 : 2·1. It is possible that the relative sizes of the oral and the ventral suckers change as the individual matures. Another character frequently used to separate species of the genus *Prosthogonimus* is the distribution of the vitellaria. *P. putschkowskii* Skrjabin, 1913 was distinguished by Skrjabin (1913) and by Witenberg & Eckmann (1939) on the grounds that the vitellaria *tend* to break into clusters. Dollfus (1948) placed *P. ovatus* in a group of species which are typified by the vitellaria forming a *more or less* continuous band. In the present collection the specimens of *P. ovatus* from *S. clypeata* all show a tendency for the vitellaria to break into clusters and in one specimen (Fig. 7) there are ten clusters on the right side and six on the left.

The most striking features of use as diagnostic criteria to distinguish species of *Prosthogonimus* are the relative positions of the ovary and the ventral sucker and the presence or absence of preacetabular uterine coils. Other characters e.g., differences in the relative sizes of the oral and the ventral suckers ; type and extent of the vitellaria ; extent of postacetabular uterine coils ; and the extent of the cirrus sac in relation to the bifurcation of the gut, should be used with extreme caution and only after a large number of specimens have been examined.

PROSTHOGONIMUS CUNEATUS (Rudolphi, 1809) Braun, 1901

Description : Body oval, length 3·62–4·81 mm., maximum breadth 1·48–2·49 mm. Cuticle scaly anteriorly, scales 9–11 microns long. Oral sucker, length 0·21–0·27 mm., breadth 0·21–0·29 mm. Prepharynx short, pharynx 0·11–0·14 mm. long and 0·09–0·17 mm. broad, oesophagus up to

0·29 mm. long. Ventral sucker, length 0·39–0·59 mm., breadth 0·38–0·56 mm., situated in anterior third of body. Testes oval, regular in outline, situated in posterior half of body. Right testis, length 0·23–0·36 mm., breadth 0·16–0·28 mm., left testis 0·19–0·33 mm. × 0·13–0·27 mm. Cirrus sac,

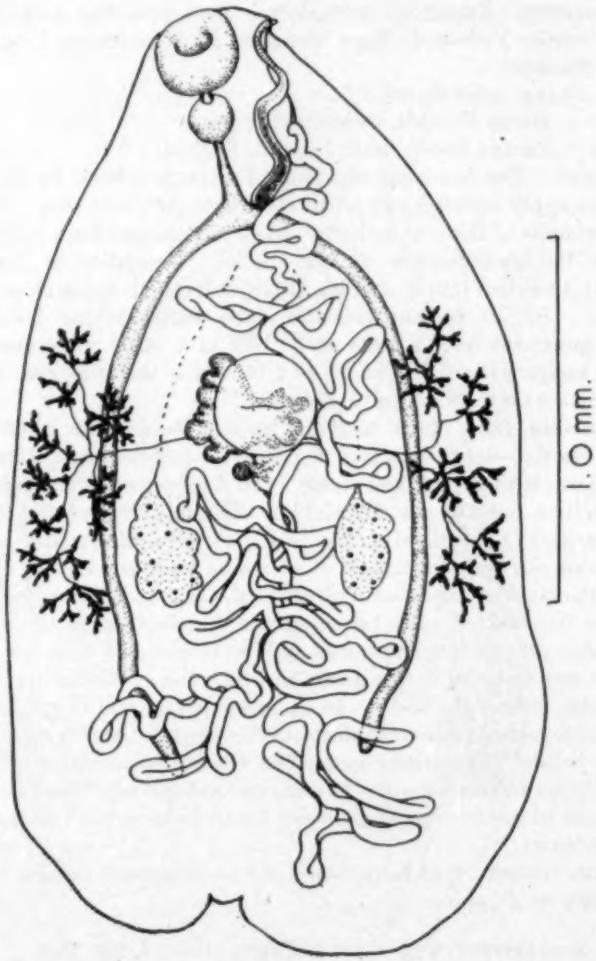

Fig. 7—*Prosthogonimus ovatus* (Rudolphi, 1803) Lühe, 1899. Entire specimen, ventral view to show the internal anatomy with the vitelline follicles arranged in clusters.

0·66–0·85 mm. × 0·08–0·11 mm., extending from about level of bifuraction of gut to the genital pore, which is on left of oral sucker. Ovary follicular, median or on right side behind ventral sucker, 0·26–0·44 mm. long and 0·22–0·44 mm. broad. Receptaculum seminis, length 0·09–0·24 mm., breadth

0·06–0·15 mm. Uterus with coiled descending and ascending limbs extending behind testes, in mature specimens, to posterior and lateral body margins. No uterine coils anterior to ventral sucker. Metraterm thin-walled. Vitellaria mainly extracaecal ; extending from ventral sucker, or a little further back, to a level just behind testes. Vitelline follicles forming a continuous band or group in clusters. Excretory pore dorsal, near posterior margin of body, excretory vesicle Y-shaped. Eggs measure 25–32 microns long by 11–16 microns in diameter.

Host : *Anas p. platyrhynchos* L.

Location : Bursa Fabricii, cloaca and rectum.

Locality : Nacton Decoy, near Ipswich, Suffolk.

Discussion : The comments made on diagnostic criteria in the discussion on *P. ovatus* apply equally well when considering *P. cuneatus*. The ratio of the measurements of the oral and the ventral suckers has been used frequently in keys for the identification of this species. According to Tseng (1932), Macy (1934), Chauhan (1940), and Ku (1940) this ratio is approximately 1 : 2 for *P. cuneatus*. In the present material some variation has been observed. Immature specimens have a ratio of 1 : 1·52 to 1 : 1·62 while mature worms have ratios ranging from 1 : 1·85 to 1 : 2·12. It is therefore essential to base an identification on fully mature specimens.

Among others, Lühe (1909) used the level of the anterior vitelline follicles to separate species—in *P. cuneatus* the anterior follicles were stated to be in front of or level with the ventral sucker. In four out of eleven specimens the anterior vitelline follicles are slightly but definitely behind the level of the posterior margin of the ventral sucker. (Fig. 8). According to Lühe's key these four specimens can be identified as *P. anatinus* Markow, 1902. Tseng (1932) considered the ratio of the measurements of the oral and the ventral suckers to be of prime importance and then used the distribution of the vitellaria to separate some of the sixteen species of *Prosthogonimus* that he recognised. *P. cuneatus* was assigned to the group in which the vitellaria from a compact band on either side of the body. In the present material two specimens have the vitellaria arranged in discrete clusters (Fig. 9) while the other specimens have continuous bands. The tendency for the vitellaria to break up into clusters may possibly be associated with the size, age and the reproductive state of the worm because immature specimens were found to have the vitellaria arranged in compact bands.

The other features that have been used as diagnostic criteria are listed in the discussion on *P. ovatus*.

SCHISTOGONIMUS RARUS (Braun, 1901) Lühe, 1909

Description : Body pyriform, length 4·45–5·26 mm., breadth 2·57–3·0 mm. Cuticle scaly anteriorly, scales up to 5 microns long. Oral sucker, length 0·34–0·39 mm., breadth 0·38 mm., pharynx 0·10–0·14 mm. × 0·19 mm., oesophagus up to 0·22 mm. long. Ventral sucker, length 0·45–0·50 mm., breadth 0·47 mm., situated in second quarter of body. Testes symmetrical, irregular in outline and situated in posterior half of body. Right testis 0·33–0·39 mm. long by 0·24–0·28 mm. broad ; left testis 0·30–0·38 mm. × 0·23–0·24 mm.

Cirrus sac elongate, length 0·71–0·75 mm., maximum breadth 0·09 mm., extending from level of bifurcation of gut to male pore, which is separate from the female pore, opening near left margin of oral sucker. Ovary deeply lobed, 0·27–0·38 mm. long and 0·49–0·52 mm. broad, partly dorsal to ventral sucker. Receptaculum seminis median, immediately posterior to ovary, length 0·12–0·14 mm., breadth 0·16 mm. Uterine folds confined to intercaecal area

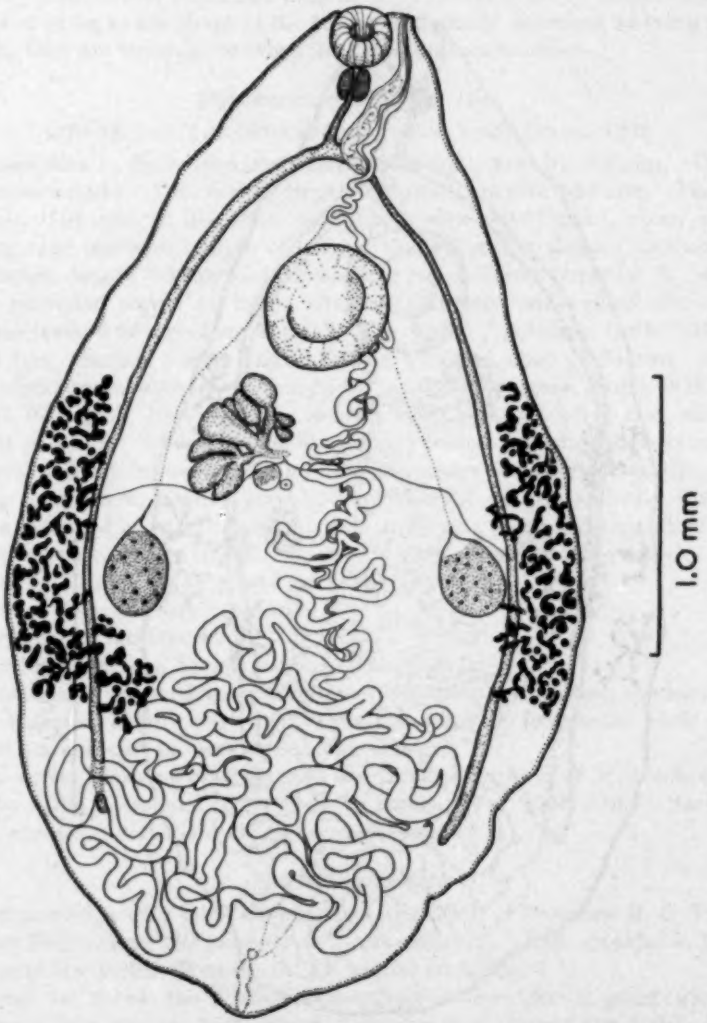

Fig. 8—*Prosthogonimus cuneatus* (Rudolphi, 1809) Braun, 1901. Entire specimen, ventral view to show the internal anatomy.

behind ventral sucker, anterior folds overlapping left caecum. Metraterm thin-walled. Female pore near posterior margin of oral sucker, about 0·3 mm. from male pore. Vitelline follicles irregular, mainly extracaecal and extending from a level anterior to ventral sucker to just behind testes. Excretory pore dorsal, situated close to posterior margin of body, excretory vesicle Y-shaped. Eggs measure 23–25 microns long by 15 microns wide.

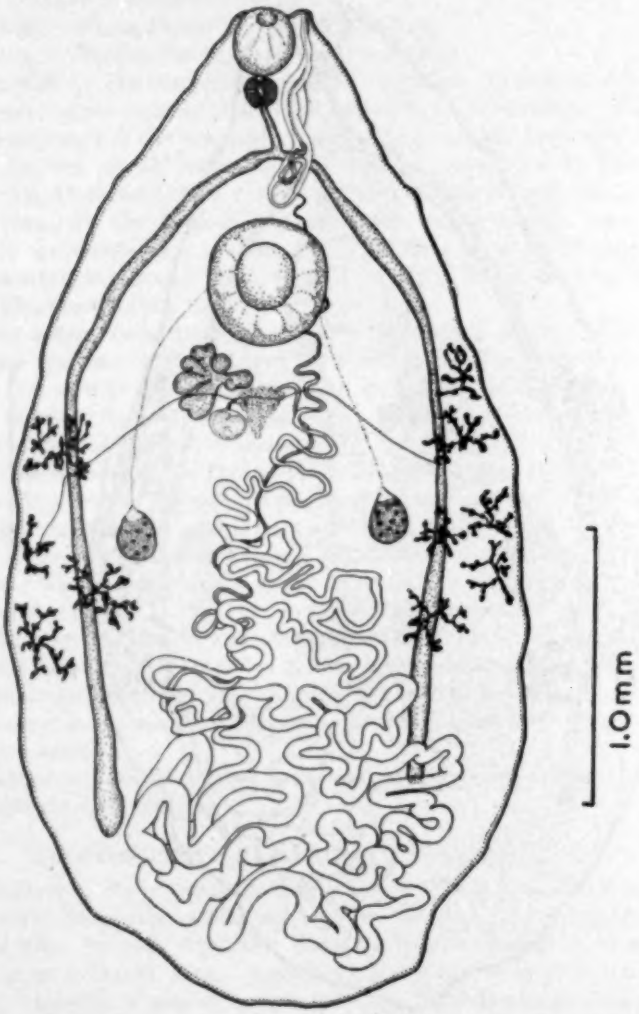

Fig. 9—*Prosthogonimus cuneatus* (Rudolphi, 1809) Braun, 1901. Entire specimen, ventral view to show the internal anatomy with the vitelline follicles arranged in clusters.

Host : *Anas p. platyrhynchos* L.
Location : Bursa Fabricii.
Locality : Nacton Decoy, near Ipswich, Suffolk.
Discussion : Two species have been included in the genus *Schistogonimus* Lühe, 1909 ; *S. rarus* (Braun, 1901) recorded from water birds in Europe and the little known *S. intermedius* Sememov, 1927 described from *Anas crecca crecca*. The present material agrees well with the description of *S. rarus* given by Lühe (1909) which has been used by Dawes (1946). Almost the only difference being in the shape of the testes ; originally described as being round or oval, they are irregular or lobed in the present specimens.

Opisthorchiidae Braun, 1901

METORCHIS XANTHOSOMUS (Creplin, 1846) Braun, 1902

Description : Body elongate, length 3·29 mm., breadth 0·5 mm. Cuticle spinous anteriorly. Oral sucker, length 0·22 mm., breadth 0·20 mm. Pharynx globular, 0·07 mm. in diameter, oesophagus short (0·07 mm.), caeca almost meeting near posterior margin of body. Ventral sucker slightly smaller than oral sucker, length 0·22 mm., breadth 0·19 mm. Testes irregular in outline, filling posterior region of body, situated obliquely one behind the other. Anterior testis 0·26 mm. long and 0·24 mm. broad ; posterior testis 0·24 mm. $\times$ 0·24 mm. Seminal vesicle long and coiled, 0·74 mm. long $\times$ 0·04 mm. Cirrus weak, cirrus sac absent. Ovary rounded, anterior to testes, length 0·16 mm., breadth 0·13 mm. Receptaculum seminis oval, 0·14 mm. $\times$ 0·08 mm. situated on right of ovary. Uterus having extensively folded ascending limb extending to a level midway between oral and ventral suckers and short descending limb leading to common genital pore just in front of ventral sucker. Vitelline follicles arranged in narrow lateral bands, overlying caeca and extending from anterior uterine coils to ovary. Excretory pore posterior and ventral. Eggs measure 25–27 microns long by 14 microns wide.
Host : *Anas p. platyrhynchos* L.
Location : Gall bladder.
Locality : Nacton Decoy, near Ipswich, Suffolk.
Discussion : According to Skrjabin (1950) there are fourteen species in the genus *Metorchis* Braun, 1901. Of these, five occur in freshwater birds while the rest are parasitic in carnivorous mammals.

The writer's specimen agrees with the brief description of *M. xanthosomus* given by Lühe (1909) and reproduced by Dawes (1946, 1956) and by Skrjabin (1950), except that the body is rather more slender.

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THE PARASITIC COPEPODA AND BRANCHIURA OF THE FISHES OF LAKE VICTORIA AND THE VICTORIA NILE

BY

GEOFFREY FRYER

*East African Fisheries Research Organization, Jinja, Uganda**

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(With 27 figures in the text)

An account is given of the parasitic Crustacea of the fishes of Lake Victoria and the Victoria Nile. Seven species of Copepoda, of which three are new, and three species of Branchiura, of which one is new, are described. Biological data are given and the fauna is discussed from a zoogeographical standpoint.

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INTRODUCTION

The following account deals with the parasitic Copepoda and Branchiura of the fishes of Lake Victoria and the Victoria Nile encountered during a sojourn of more than two years on the shores of the lake. Although the fish fauna of this, the largest of the African Lakes, is now fairly well known, relatively little has been recorded concerning the parasites of these fishes. This paper

* Present address : Freshwater Biological Association, Far Sawrey, Ambleside, Westmorland.

attempts to fill this gap in our knowledge so far as the parasitic crustaceans are concerned. Most of the specimens examined were collected in the vicinity of Jinja which lies near to the point at which the infant Nile leaves the lake, but nevertheless samples of most of the fishes inhabiting the lake have been examined and it is believed that, faunistically, our picture of their crustacean parasites is reasonably complete.

Earlier collections had already brought to light the existence of crustacean parasites in the lake. The work of Stuhlmann (1891), Mrázek (1898) and Cunnington (1913) revealed successively the presence of *Dolops ranarum* Stuhlmann, an unidentified ergasilid copepod, and *Argulus africanus* Thiele, while Graham (1929), besides observing the first and last of these, reported the occurrence of a *Lernaea* which Cunnington characterised as a "Nilotic species", without however, giving it a name. The present investigations have added several species to this list, some of which are here described as new. Material of all these new species is deposited at the British Museum (Natural History).

SYSTEMATIC AND BIOLOGICAL NOTES

The following species have been found during the course of the investigations :—

COPEPODA
- Family Ergasilidae
  - *Ergasilus lamellifer* sp. n.
- Family Lernaeidae
  - *Lamproglena monodi* Capart
  - *Lamproglena clariae* Fryer
  - *Lamproglena barbicola* sp. n.
  - *Lernaea barnimiana* (Hartmann)
  - *Lernaea cyprinacea* s. lat. L.
  - *Lernaea inflata* sp. n.

BRANCHIURA
- Family Argulidae
  - *Argulus africanus* Thiele
  - *Dolops ranarum* (Stuhlmann)
  - *Chonopeltis brevis* sp. n.

Each species is dealt with in turn in the following account.

COPEPODA

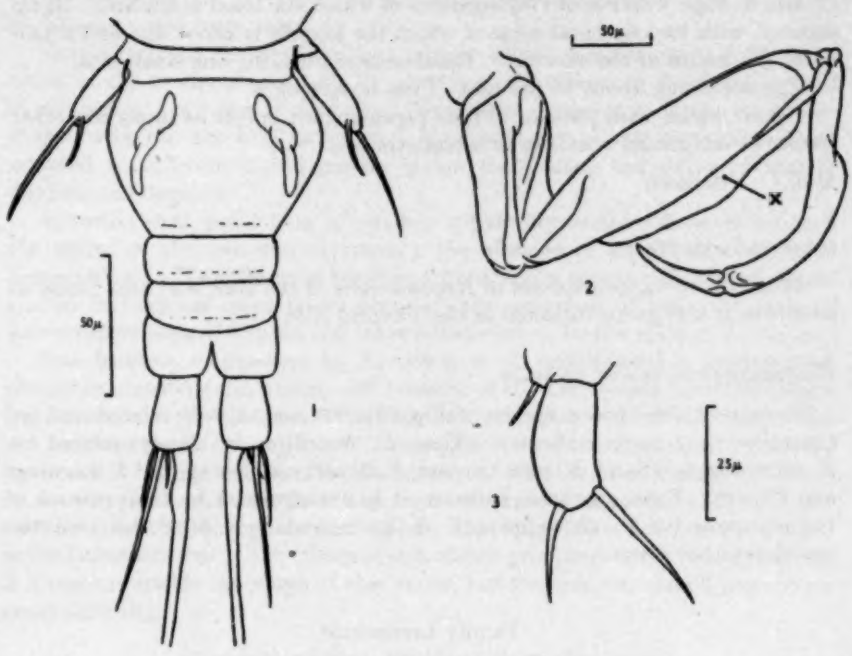
Family Ergasilidae

Only one member of this family, an apparently undescribed species, has been found in the lake. This is described below :—

ERGASILUS LAMELLIFER sp. n. (Figs. 1–3)

Adult female

Length to about 850μ. Cephalothorax fused to somite of leg 1, longer than wide, bluntly rounded anteriorly, and shallowly indented in posterior third. Head sculpture consisting of an inverted T, anterior and posterior to which



Figs. 1–3.—*Ergasilus lamellifer* sp. n.
1. Posterior region of body. Ventral. Female. 2. Antenna. 3. Leg 5. X. Chitinous lamella.

are circular to ovoid markings very similar to those of *E. macrodactylus* (Sars) and several other species of the genus. Somites of legs 1 to 5 distinct. Abdomen of three somites. Genital somite wider than long and bulged laterally so as to be widest a little way anterior to the middle. Last two abdominal somites very short. Furcal rami simple, about one and a half times as long as wide, and armed with four unjointed terminal setae. Innermost seta longest and rather more than two and a half times as long as next longest. Longest seta swollen and somewhat "kinked" near the base (Fig. 1). Antennule of six segments. Antenna prehensile and of form shown in Fig. 2. Along the inner margin of segment 2 is a thin, blade-like chitinous lamella.

Legs 1–4 of structure typical for genus and having the following arrangement of spines and setae :—

P1	Exopod	1–0	1–1	2–5
	Endopod	0–1	0–1	2–4
P2	Exopod	0–0	0–1	0–6
	Endopod	0–1	0–2	1–4
P3	Exopod	0–0	0–1	0–6
	Endopod	0–1	0–2	1–4
P4	Exopod	1*–0	0–5	
	Endopod	0–1	0–2	1–3

* Indicates that the spinule is very small.

Leg 5 (Figs. 1 and 3) of two segments of which the basal is minute. Distal segment with two terminal setae of which the longest is about one and a half times the length of the shortest. Basal segment bearing one small seta.

Egg sacs long, about 75 per cent of the body length.

Colour white, with patches of blue pigment (not purple as in certain other species of the genus) ventrally in cephalothorax.

Male : Unknown.

Hosts and occurrence

Common on various species of *Haplochromis* in the lake, and also found on members of this genus collected in the Victoria Nile.

Diagnostic features and affinities

Several of the African species of *Ergasilus* are very closely related and are separable only with difficulty. Thus *E. lamellifer* is closely related to *E. macrodactylus* (Sars), *E. sarsi* Carpart, *E. kandti* van Douwe, and *E. cunningtoni* Capart. From all these, however, it is distinguished by the presence of the chitinous limella on segment 2 of the antenna. It is to this that the specific epithet refers.

Family Lernaeidae

A note on the systematic position of the genus Lamproglena

In this paper I place the genus *Lamproglena* in the family Lernaeidae and not in the Dichelesthiidae. In doing so I follow Sproston, Yin & Hu (1950) who proposed this change in a not readily accessible paper. These authors pointed out the great similarity of the males and larvae of *Lamproglena* to those of *Lernaea*, and the differences between *Lamproglena* and the other members of the Dichelesthiidae. Having seen males and larvae of both genera, and in fact having alluded to the great similarity of their males (Fryer 1956), and having consulted the definition of the family Dichelesthiidae given by Wilson (1922) I agree with Sproston *et al.* that *Lamproglena* should be removed from the Dichelesthiidae and its affinities with *Lernaea* recognised. This can only be done by putting them in the same family and, although there are striking differences between the adult females, which Sproston *et al.* recognised by the erection of a new sub-family—the Lamprogleninae—this seems justified. These differences are to be interpreted as reflecting the fundamentally different types of parasitism practiced by the adult females, *Lamproglena* being a gill parasite and *Lernaea* settling elsewhere. This has led to the development of different methods of attachment and the development in *Lernaea* of the very striking cephalic horns which comprise the anchor. In spite of this and other great differences there exist what appear to be fundamental similarities between the two genera such as the elongation of the thorax and its tendency to lose segmentation after settlement. In this respect

Lamproglena clariae Fryer goes some way towards showing how the condition in *Lernaea* could have arisen.

One difference between the two genera whose significance is difficult to assess is the production of eggs in uniseriate egg strings in *Lamproglena* and in multiseriate egg sacs in *Lernaea*. This again, however, may not be unconnected with the site of attachment ; the two types of egg suspension being adapted to different environments rather than being indicative of remote phyletic relationship.

Sproston *et al.* point to a trivial but apparently useful difference between the males of the two genera, namely the absence of an antennal hook in *Lamproglena*. The difference between a hook and a seta is only one of degree and in fact one or more hooks occur on the antennae of both the male of *Lamproglena monodi* Capart and what is believed to be the male of *L. clariae*.

The features emphasised by Sproston *et al.* necessitated a fundamental change in classification, namely the transfer of the Lernaeidae from the Caligiformes to the Cyclopiformes of Oakley's classification. As these authors did not have access to Gurney's (1933) monograph they were unable to consider how such a change would affect his system. All that is necessary in fact is to remove the Lernaeidae from the Lernaeiformes of the order Caligoida and transfer it to the Cyclopoida leaving only the Sphyriidae and Lernaeoceridae in the Lernaeiformes. The effects of this on sub-groupings within the Cylopoida is a matter outside the scope of this paper, but the transfer should present no great difficulty.

LAMPROGLENA MONODI Capart (Fig. 4)

This parasite of cichlid fishes is widely distributed in all four of the major river systems of Africa. In Lake Victoria it is not uncommon on species of *Tilapia* and *Haplochromis*, though infestations seldom seem to be heavy. It has also been found on the few specimens of *Haplochromis* spp. which have been available from the Victoria Nile. Although the numbers dealt with from the river were too small to be significant the indications were that infestations may be heavier here than in the lake.

Neither the adult male nor larvae of this species have been described. Both have been found in Lake Victoria. The only adult male collected was found associated with an adult female attached to the gills of *Haplochromis* sp. Its general appearance is shown in Fig. 4 which renders a detailed description unnecessary. Points meriting notice are the two-segmented nature of the rami of the swimming legs and the fact that, although only three terminal spines are readily apparent on the maxillipeds, five are actually present, two being detectable only as a result of careful focusing.

Copepodid larvae representing either the last or penultimate copepodid stage and the preceding stage were also found associated with adult females on the gills of fishes. These differed but little from the adult male except in the genital region. Even the oldest of these stages had only two-segmented rami. Whether a subsequent moult to give a further copepodid stage with three-segmented rami takes place is not known, but the structure of the mouthparts of these late larvae suggested that the next moult would be the last.

Fig. 4—*Lamproglena monodi* Capart. Adult male, ventral.

LAMPROGLENA CLARIAE Fryer

This species, which has hitherto been recorded only from Lake Nyasa (Fryer 1956), has been collected on several occasions from the gill filaments of *Clarias mossambicus* in Lake Victoria. Only light infestations have been encountered. While in Lake Nyasa this species is fairly constant in structure, in Lake Victoria there is considerable variation in size and proportions. In Lake Nyasa the maximum length is about 9 mm. and specimens are seldom very much shorter than this, but in Lake Victoria the size range observed is from about 5·9 to 10·1 mm. In Lake Nyasa the abdomen and telson combined comprise about 42 per cent of the total length and there is no noticeable variation in this respect but in Lake Victoria this portion of the body comprises from 41 to 52 per cent of the total length, with the higher values predominating. In the larger specimens this imparts a markedly elongate appearance to the posterior portion of the body and gives the superficial appearance of a different species when such specimens are compared with their more abbreviated brethren.

A few specimens of this species have recently been taken from the gills of *Heterobranchus longifilis* Cuvier and Valenciennes, another clariid fish, collected at Iragalla in the Malagarasi swamps. These are much smaller

than the specimens from either Lake Nyasa or Lake Victoria and have a total length of only 4·0 mm. It would appear therefore that, like *L. monodi*, *L. clariae* is a very variable species.

In Lake Nyasa males tentatively assigned to *L. clariae* were described (Fryer 1956). In Lake Victoria similar males have been found associated with females of *L. clariae*, thus making it almost certain that they are indeed males of this species.

LAMPROGLENA BARBICOLA sp. n. (Figs. 5–10)

Adult female

Length to about 5 mm. Body grub-like in general appearance (fig. 5); segmentation quite well marked. First leg-bearing thoracic somite not incorporated into cephalothorax, which is wider than long. Cephalothorax comprising about 10 per cent of total length. Median eye distinct : red in life.

Thoracic somites 1–4 progressively increasing in size ; somite 1 being very small and narrow. Somites 3 and 4 greatly enlarged, somite 5 present, very much smaller than somite 4 and smaller than genital somite, but quite distinct.

Abdomen of three distinct somites. Genital somite expanded laterally and wider than long. Genital apertures situated laterally. Telson elongate, and a trifle shorter than abdominal somite 3. Furcal rami short, simple, papillate, and each bearing a small terminal papilla.

Antennule (Fig. 8) short, flattened and reduced to two distinct and one indistinct segments. Basal segment much longer than distal and lacking the anterior fringe of setae usually present in other species of *Lamproglena*. Antenna (Fig. 9) approximately as long as antennule and four-segmented. Basal segment comprising almost half total length and fringed distally by a characteristic crown of spinules. Oral region surrounded by a wide-walled, horseshoe-shaped, sucker-like structure.

" Maxilla " long and strap-like and with a single scleratized tooth distally. Tips of opposing appendages overlapping slightly.

Maxilliped stout, strongly reflexed, and bearing three recurved distal spines.

Ventral surface of head between maxillae and maxillipeds sclerotized in form of an X with branched anterior arms (Fig. 6).

Thoracic legs 1 to 4 of similar structure (Fig. 10). All biramous and showing partial obliteration of segmentation, and all with much reduced setation.

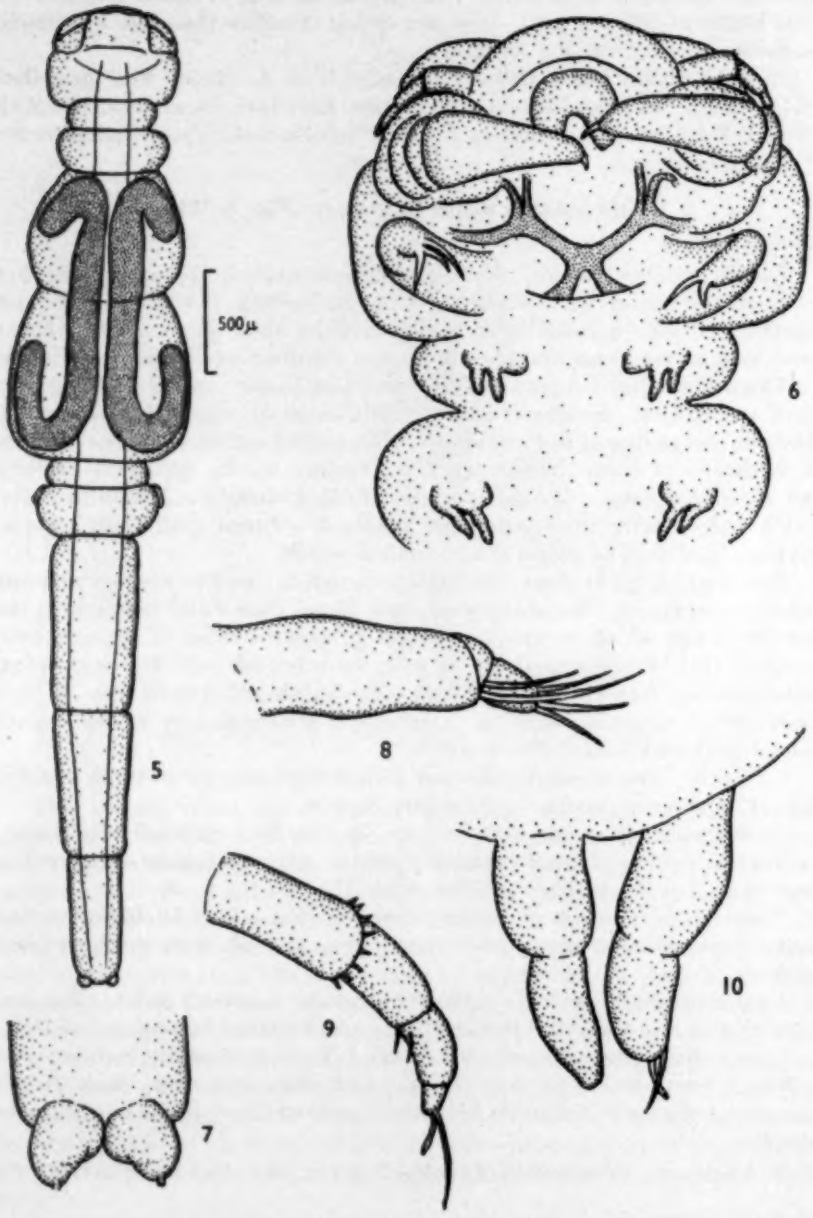
Eggs maturing in oviducts confined to thoracic somites 3 and 4. Egg sacs consisting of long uniseriate chains of eggs which extend beyond end of body.

Colour dirty white tinged with brown. Eggs in oviducts showing pale yellowish brown : in egg sacs darker. Gut often appearing black due to presence of pigmented spherules in its walls, and red due to presence of ingested blood.

Male: Unknown. Syntypes: B.M.(N.H.) Reg. No. 1961.5.9.4 and 5, in B.M.Coll.

Host and occurrence

Several specimens have been found on the gills of the cyprinid fish *Barbus altianalis radcliffi* Boulenger captured in the lake itself, but none have yet



Figs. 5–10—*Lamproglena barbicola* sp. n.
5. Adult female. Dorsal. 6. Cephalothorax and thoracic somites 1 and 2. Ventral. 7. Tip of abdomen and furcal rami. Ventral. 8. Antennule. 9. Antenna. 10. Leg 2.

been recorded from specimens of this fish taken from the Victoria Nile. Infestations do not usually exceed half a dozen specimens.

Diagnostic features

This species can be separated from other African members of the genus, and from the Palaearctic *L. pulchella* Nordmann, to which it is similar in many respects, by the absence of an anterior fringe of setae on the antennule.

LERNAEA BARNIMIANA (Hartmann)

Specimens which can be assigned without hesitation to this variable and widespread African species occur frequently on *Barbus altianalis radcliffi* Boulenger but show interesting differences in abundance and site preference according to the habitat frequented by the host.

In the Victoria Nile just below the Owen Falls Dam it is extremely common on hosts over about 25 cm. in length. Below this size of host it is not particularly common and the degree of infestation appears to be low : above it it is very rare to find an uninfected fish and heavy infestations are common. By far the commonest site of attachment in river-dwelling hosts is the buccal cavity, and here as many as 106 specimens have been found in a 58 cm. fish. As the entire anchor, the tips of whose longest (dorsal) arms may be as much as 1 cm. apart, is embedded in the flesh of the host, such heavy infestations are obviously very serious, and these parasites undoubtedly contribute to the very poor condition of many of the large *Barbus* taken from the river. Suppuration of the wound caused by the anchor is the rule and the area of flesh surrounding the anchor is so soft and digested that the parasites are very easily pulled out with intact anchors. Attachment to other sites, while observed on several occasions, is much less common, and particularly so when compared with attachment within the buccal cavity. In the lake, on the other hand, the infestation rate is very much lower and many large *Barbus* are uninfected. When *L. barnimiana* is present it is rarely attached within the buccal cavity but selects other sites such as the base of the fins or the heavily scaled flanks. The reason for this difference in site selection in the two populations is not known, but currents flowing in the river may militate against the attachment of larvae to external sites.

Differences in the site of attachment exert a very profound effect on the shape of the anchor of this species, a topic which has been dealt with elsewhere (Fryer 1961a).

In addition to occurring on *Barbus* this species is found in Lake Victoria, though rarely, on species of *Tilapia* and on *Labeo victorianus* Boulenger.

LERNAEA CYPRINACEA s. lat. L.

Reasons for equating a form from Lake Victoria with *L. cyprinacea*, and therefore recording this species from Africa for the first time, have been given elsewhere (Fryer 1961a). In Lake Victoria this species is not uncommon on both the indigenous species of *Tilapia* (being more common on *T. variabilis* Boulenger than on *T. esculenta* Graham) and shows a marked predilection for the jaws where up to sixty-six specimens have been found on a single host.

It is found rarely on the flanks of these species and rarely on other cichlid fishes of the genus *Haplochromis*. Its extreme variability has been discussed and illustrated elsewhere (Fryer 1961a).

Copepodid larvae of this species have been found to be extremely common on the gills of *Bagrus docmac* Forskal. Their identity was established by infecting with them *Tilapia* kept in tanks. On these fishes adult females bearing egg sacs were reared in less than seven days at a temperature of approximately 25°C. A single host sometimes carries several hundred larvae. These, incidentally, are most easily collected by holding the head of the fish over a suitable receptacle, directing a powerful jet of water onto the gills for a few seconds, and placing this water in a dish which is illuminated at one corner. The larvae are positively phototactic ; congregate there, and can be removed with a pipette. Although the older copepodid stages predominated in these collections several stages were seen, indicating that most, if not all, post-naupliar stages are by choice parasitic in habits. The biological significance of this intermediate host, the location of which would appear to double the hazards involved in this critical process, is unknown.

LERNAEA INFLATA sp. n. (Figs. 11–21)

Adult female

Length to 7·8 mm.

Head rounded and elevated above anchor arms. Anchor with a pair of unbranched ventral arms and a pair of longer, typically unbranched, dorsal arms (branched in one specimen). Ventral arms variable in length ; sometimes very short and swollen (Figs. 13 and 14) sometimes more tubular (Figs. 11, 12 and 19) but usually distinctly shorter than dorsal arms. Dorsal arms usually distinctly swollen medially and, in one specimen, with very distinct outgrowths from swollen region (Figs. 11 and 12).

Thorax cylindrical, characteristically exhibiting a gentle curvature between legs 2 and 3, and increasing gradually in diameter towards posterior end which is often distinctly swollen in vicinity of pregenital prominence. Thorax with a small but distinct lateral outgrowth in the vicinity of leg 2. (Figs. 12–15 and 19).

Pregenital prominence usually very distinctly double (Figs. 13, 20 and 21) but virtually simple in specimen with forked anchor arms (Fig. 16). Abdomen simple and tubular, usually showing very faintly its three-somited origin. Remains of furcal rami and setae present.

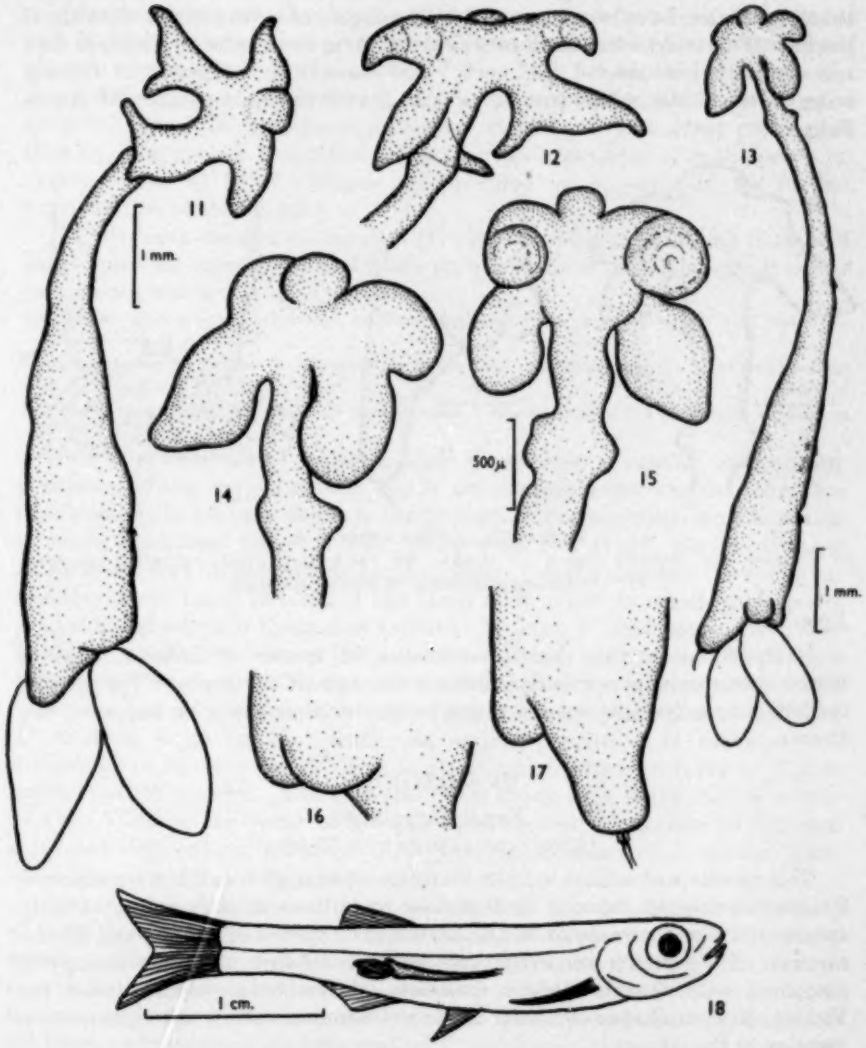
Legs located at approximately 6, 16–19, 39–45 and 76–78 per cent of distance along body. Torsion usually slight and generally confined to region between legs 2 and 3, where it is sometimes dextral, sometimes sinistral.

Armature of legs as in *L. cyprinacea* and most other species of the genus, i.e. with five setae on distal segment of exopod of each leg.

Egg sacs rather elongate when fully developed, shorter when newly produced.

Cuticle practically colourless, but tinged with brown. Gut showing through very darkly due to presence in the walls of dark granules. Eggs in oviduct pale emerald green. Eggs in egg sacs bright emerald green.

Holotype : B.M.(N.H.) Reg. No. 1961. 5.9.1.—and paratypes in B.M.Coll.

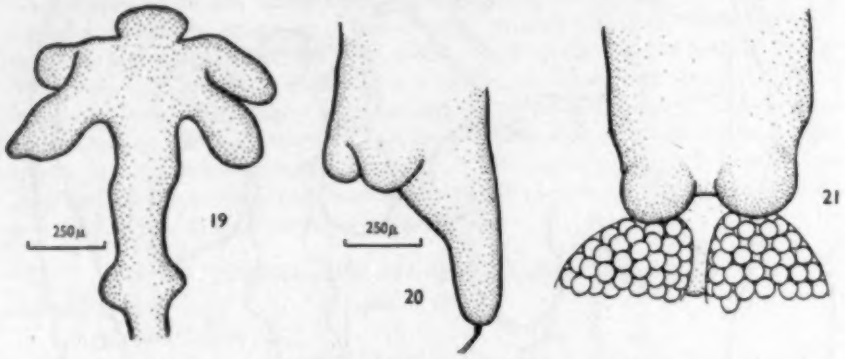


Figs. 11–18–*Lernaea inflata* sp. n.

11. Adult female. 12. Anchor of same specimen. 13. Adult female. Holotype. 14. Anchor and anterior region of thorax of holotype. Almost dorsal. 15. Anchor and anterior region of thorax of holotype. Ventral. 16. Pregenital prominence of specimen shown in fig. 11. 17. Abdominal region. Another specimen. 18. Adult female *in situ* on flank of *Engraulicypris argenteus*.

Host and Occurrence

Engraulicypris argenteus (Pellegrin). Only a few individuals of this species have been collected although several hundred specimens of the host, which is a shoaling species, have been examined. The degree of infestation at the time of the year (February) when the host was available in abundance in the Jinja area was certainly less than 1 per cent. The hosts were collected in flowing water in the Victoria Nile just below the site of the now submerged Ripon Falls.



Figs. 19–21—*Lernaea inflata* sp. n.
19. Anchor and anterior region of thorax. 20. Abdominal region of same specimen. 21. Pregenital prominence of another specimen.

Remarks

It is difficult to find descriptive names for species of *Lernaea*, most of whose characteristics are fairly constant throughout the genus. The specific epithet chosen for this species refers to the swollen posterior region of the thorax.

BRANCHIURA

Family Argulidae

ARGULUS AFRICANUS Thiele

This species is abundant in Lake Victoria. Although it exhibits a preference for smooth-skinned fishes it finds similar conditions in the mouths of scaly species and is not uncommon in this situation on species of *Tilapia* and *Haplochromis*. Data on its occurrence are presented below when its ecology is compared with that of *Dolops ranarum*. It has been recorded from the Victoria Nile on *Barbus altianalis* but is not common on this host either in the river or in the lake.

DOLOPS RANARUM (Stuhlmann)

This species is also abundant in Lake Victoria where it not infrequently coexists with *A. africanus*. Its ecology is most conveniently dealt with in a comparative manner. It has been recorded also from the Victoria Nile on one of the few specimens of *Bagrus docmac* collected in the river.

The comparative ecology of Argulus africanus *and* Dolops ranarum *in Lake Victoria*

Observations made elsewhere in Africa in regions where both *A. africanus* and *D. ranarum* occur have revealed differences in the ecological preferences of the two species (Fryer 1956 ; 1959 ; 1960). Both are capable of parasitising many different hosts and it already seemed apparent that, within the range of tolerated hosts, the parasite is influenced more by their habitat preferences than by their specific properties. The frequent occurrence of both species on various fishes of Lake Victoria has provided an opportunity for further consideration of this problem.

Of the hosts the five commonest provide the most illuminating data. Of these, three are smooth skinned fishes on which the relative abundance of the two species was found to be as follows :—

Protopterus aethiopicus Heckel—*D. ranarum* predominates. Approximately 11·8 times as abundant as *A. africanus*.

Clarias mossambicus Peters—*D. ranarum* predominates. Approximately 4·4 times as abundant as *A. africanus*.

Bagrus docmac Forskal—*D. ranarum* predominates. Approximately 5·3 times as abundant as *A. africanus**.

Previous observations indicated that *D. ranarum* is capable of tolerating conditions of low oxygen tension and it was suggested that the red coloration of this species in life may be due to the presence of haemoglobin—an adaptation to these conditions (Fryer 1956). Since then Fox (1957) has shown that *D. ranarum* does indeed possess haemoglobin. Consideration of the ecological distribution in Lake Victoria of the three main hosts on which this species predominates supports these observations. Thus on *P. aethiopicus* and *C. mossambicus*, which, by virtue of the possession of lungs and accessory respiratory organs respectively, are able to tolerate conditions of low oxygen tension, and which are bottom dwellers which also frequent swampy margins of the lake, *D. ranarum* is by far the commonest argulid parasite. *D. ranarum* also predominates on *B. docmac*. This is a fish which often ventures to depths greater than 30 metres. Now Fish (1957) has shown that, in the inshore waters of Lake Victoria, the water at a depth of 30 metres is less than 50 per cent saturated with oxygen for most of the year, so parasites of *B. docmac* must often be exposed to low oxygen tensions.

The relative abundance of these parasites on the two indigenous species of *Tilapia*, neither of which frequents areas of low oxygen tension to the same extent as the three previously mentioned hosts, is quite different. In neither case is *D. ranarum* particularly common and, as Table 1 shows, on both these fishes *A. africanus* is the commonest species. It is most abundant (and about 8·6 times as frequent as *D. ranarum*) on *T. esculenta* Graham which frequents the open waters of sheltered bays where there is an abundance of oxygen. Being a phytoplankton feeder *T. esculenta* seldom ventures to depths of 30 m. and indeed the main fishing grounds for this species are in areas where the water is less than 30 m. deep.

* A peculiar case in which 272+ specimens of *A. africanus* were counted on a specimen of *B. docmac* has been ignored as this was obviously due to peculiar circumstances and would wrongly bias the general picture.

Table 1—Average number per fish of specimens of *Argulus africanus* and *Dolops ranarum* on 630 specimens of *Tilapia variabilis* and 342 specimens of *T. esculenta* of the size caught in gill nets of 4½ inch mesh and above.

	Argulus africanus	*Dolops ranarum*
Tilapia variabilis	0·63	0·28
Tilapia esculenta	3·17	0·37

On *T. variabilis* Boulenger, which is less of an open-water species than *T. esculenta*, it is considerably less abundant, and only about 2·3 times as frequent as *D. ranarum*.

From these and previous data one can fix the broad ecological preferences of these species with considerable precision. *D. ranarum* is a species of swampy or turbid waters which becomes progressively less abundant in open-water situations, though it appears to be greatly assisted in the colonisation of such habitats by turbid conditions, and is apparently precluded from occurring in the clear open waters of the northern part of Lake Nyasa in whose vicinity it occurs. The ecological preferences of *A. africanus* are broadly the reverse of this and this species favours the more open-water environments, though it has by no means adapted itself to the role of a parasite of truly pelagic fishes. In many areas, such as Lake Victoria, there is a zone of considerable overlap between the two species.

Although the two parasites frequently occur together on the same host there is often, as a result of preferences for particular sites of attachment, a certain amount of isolation between them, and they differ in feeding habits. Also they tend to occur in monospecific aggregations. *D. ranarum* tends to creep into crannies between folds of skin and into confined spaces generally e.g. into the crannies provided where the opercular bone takes its origin from the head, and it shows a particular predilection for the small and greatly sheltered gill cavity of *Protopterus*. Also, although both species occur in regions where bone is covered with skin—particularly the head region and inside the mouth—*D. ranarum* seeks out areas where a thick layer of flesh with a well-marked blood supply overlies the bone, while *A. africanus* very often occurs in regions where the bone is covered only by a thin layer of skin. This distribution is probably correlated with feeding habits. *D. ranarum* pierces the flesh and actually sucks blood while *A. africanus* appears to feed only on mucus.

There seems to be a correlation between the size of the fish and the number of argulids carried : the larger the fish the larger the number of parasites likely to be present.

CHONOPELTIS BREVIS sp. n. (Figs. 22–27)

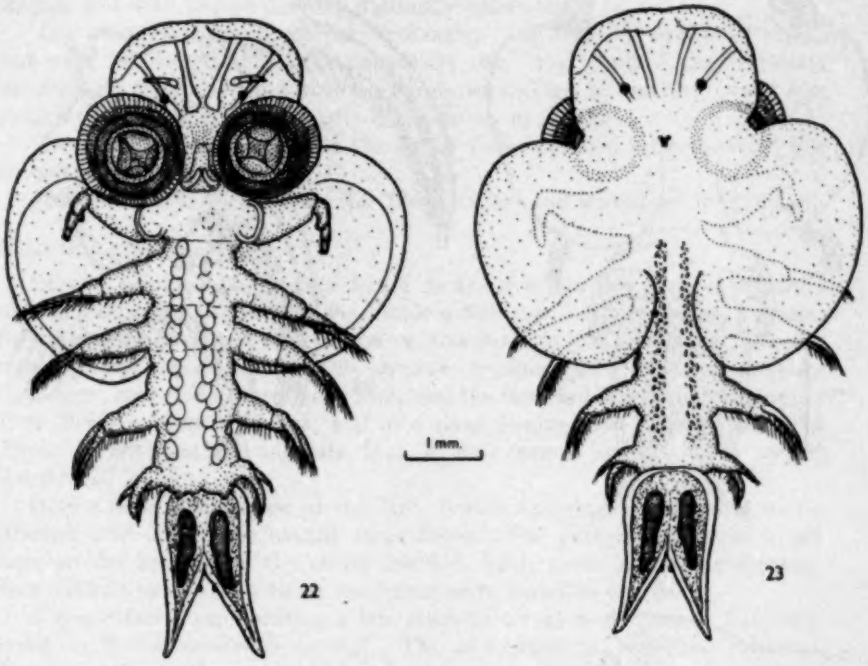
Adult female

Length to about 8·5 mm.

General appearance rather squat. Carapace trifoliate, reaching back so as usually to obscure bases of second pair of legs, and comprising some 57 per cent of total body length. Width of anterior (cephalic) lobe of carapace a little less than half maximum carapace width. Respiratory areas of carapace

similar to those of other species of the genus. Eyes small. Ocellus small and forming with the eyes a more or less equilateral triangle.

Abdomen comprising some 27 per cent of total body length. Furcal rami minute, situated near base of abdominal lobes.



Figs. 22–23—*Chonopeltis brevis* sp. n.
22. Adult female. Holotype. Ventral. 23. Holotype. Dorsal.

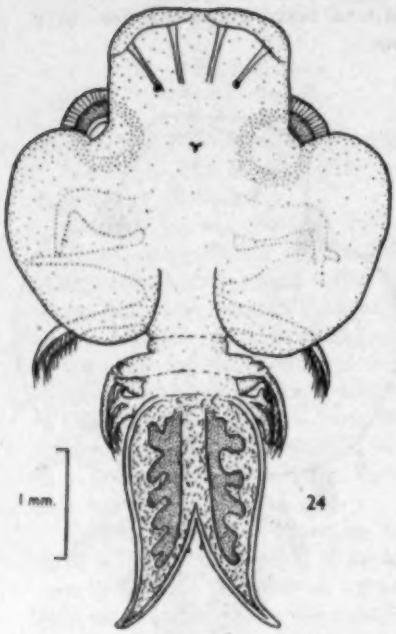
Anterior appendages, including suckers, very similar to those of other species of genus. Sucker diameter about 28 per cent of the carapace width.

Maxilla rather short : not prehensile.

Legs 1 to 3 similar in structure. Leg 1 slightly longer than leg 2, which in turn is slightly longer than leg 3. Leg 4 similar to preceding legs but very much smaller. " Natatory lobe " broadly rounded and somewhat drawn out laterally where it overlies a backwardly projecting papilla of the coxa.

Spermathecae elongate and extending posteriorly beyond point of bifurcation of abdominal lobes.

Almost colourless and transparent—in contrast to other species of genus which are milk white—save for contents of spermathecae and eggs in uteri which are white, and for two bands of small black pigment spots overlying the latter.



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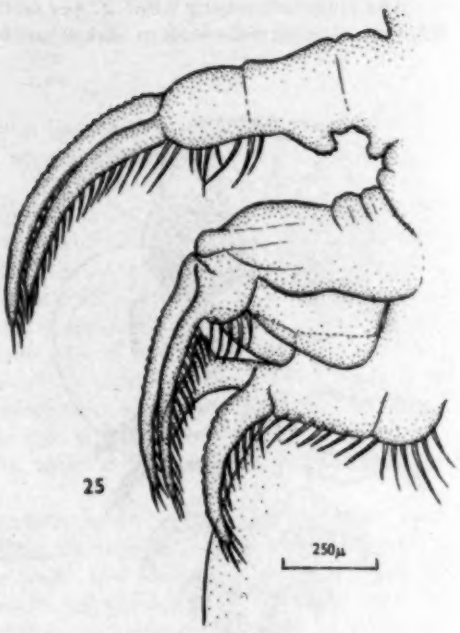

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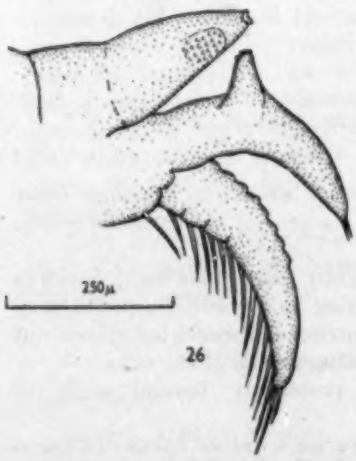

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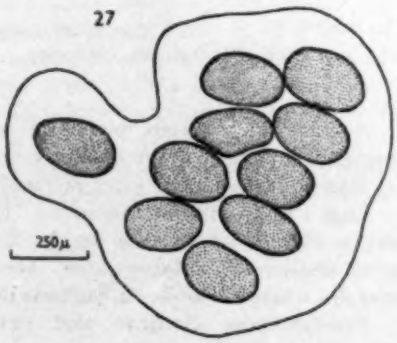

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Figs. 24–27—*Chonopeltis brevis* sp. n.
24. Adult male. Dorsal. 25. Legs 2, 3 and 4. Male. Ventral. 26. Leg 4 male. Dorsal.
27. Cluster of eggs.

Adult male

Length to about 6 mm.

General form similar to that of female but with much larger and more conspicuous abdomen. Length of carapace some 55 per cent of total length. Abdomen much wider than in female, comprising some 38 per cent of total length, and with its tips directed distinctly outwards.

Leg 1 similar to its counterpart in female. Leg 2 similar to that of female but with two roughened studs posteriorly (Fig. 25). Legs 3 and 4 greatly modified for copulation and having form shown in Figs. 25 and 26. Testis sacs elongate and having characteristic shape shown in Fig. 24.

The specific epithet refers to the rather fore-shortened appearance of this species.

Holotype: B.M.(N.H.) Reg. No. 1961. 5.9.6.—and paratypes in B.M.Coll.

Hosts and occurrence

Several specimens have been found on the cyprinid fish *Barbus altianalis radcliffi* Boulenger collected in the Victoria Nile just below its point of origin. No specimens have yet been found on this host in the lake itself, but one specimen has been taken from another cyprinid fish, *Labeo victorianus* Boulenger, collected in the lake. This, and the fact that it occurs in the upper Tana River system in Kenya, and in a river flowing into Lake Tanganyika (Fryer in preparation) suggests that it may prefer conditions in rather fast-flowing water.

Only a small proportion of the Nile *Barbus* examined were found to be infected, and these were usually large fishes. The parasites occurred in all cases on the belly or on the pelvic fins and, being more or less transparent, were difficult to see. Up to six specimens were found on one fish.

A single larva, representing a late stage in larval development, has been found on *Barbus altianalis radcliffi*. This is exceptional and data collected elsewhere indicate that some other fish will serve as larval host in the Victoria Nile, for it has recently been found that all the larval stages, like the adult, are parasitic in habits (Fryer 1961).

Eggs

Several groups of eggs (Fig. 27) have been deposited in glass dishes by females. Unfortunately, although these became embryonated, none ever hatched. The eggs were deposited in groups of from seven to twenty-two and differed rather markedly from those of *C. inermis* Theile already described (Fryer 1956). Eggs are ovoid but are less regular in shape than are those of *C. inermis* and have axes measuring 291–313μ and 156–172μ. They are white when laid but quickly become darker. Each egg is surrounded by an egg membrane but there is no thick gelatinous outer layer such as occurs in *C. inermis* and which, after hardening, forms in that species a very characteristic protective layer. As a result the eggs are located closer to each other than in *C. inermis* and in this they resemble several species of *Argulus*. In fact, some eggs actually touch each other and this plays some part in their distortion. A cement layer, which eventually becomes amber in colour, is present as in *C. inermis*.

General remarks

Like other members of its genus *C. brevis* is incapable of swimming, but when its weight is supported on the bottom of a glass dish it can propel itself forward by beating its legs. In life legs 1 and 2 of the female beat briskly and leg 3 beats slowly and ineffectively. In the male only legs 1 and 2 beat.

Affinities

C. brevis, *C. inermis*, and a species to be described later as new, constitute a trio of closely related but nevertheless distinct species. The similarities are most apparent in the case of the females between which differences tend to be quantitative rather than qualitative and seem to be associated with a tendency for the body to be foreshortened in *C. brevis* and elongate in the other two species. In spite of the great morphological similarities of the females it is interesting that the eggs of *C. brevis* and *C. inermis* are very different.

The males are more obviously distinct than the females but, while the " peg and socket " apparatus of legs 3 and 4 shows distinct differences in the three species (e.g. the peg is cylindrical in *C. inermis* and conical in *C. brevis*) it is easy to see how the conditions found in all three, and in *C. congicus* Fryer, to which *C. brevis* is also quite closely related, could have been derived from a common type. The clasping apparatus of the males of these four species represent variations on a common theme.

GEOGRAPHICAL DISTRIBUTION

Of the ten species of parasitic crustaceans recorded from Lake Victoria, four (*Lamproglena monodi*, *Lernaea barnimiana*, *Argulus africanus* and *Dolops ranarum*) are pan-African in distribution. One other, *Lamproglena clariae*, is known from Lake Nyasa and the Malagarasi swamps and may also prove to be widespread. The host distribution of the copepods described as new suggests that one at least (*Lamproglena barbicola*) will probably be found to occur elsewhere in the Nile system, but the other two could conceivably be endemic.

The presence of *Lernaea cyprinacea* indicates that transmigration to or from Eurasia via the Nile system has been possible in the past, (see Fryer 1961a).

The most interesting species from the point of view of zoogeography is the branchiuran *Chonopeltis brevis* which has already been found in the Tana River system, Kenya, and in the Mugambuzi River which flows into Lake Tanganyika (Fryer 1961, and in preparation). This faunistic similarity indicates a possible former connection of the Lake Victoria basin with eastward-flowing rivers, that is, rivers east of the eastern branch of the great rift, and offers valuable support to the evidence so far available from fish distribution (see Whitehead 1959).

When compared with the Nile below Lake Albert and with the lakes in the upper part of the drainage area of that river, which are still incompletely explored, the parasitic crustacean fauna of Lake Victoria is definitely impoverished, for at least twelve species known from that area are apparently absent from its fauna. (Some of the records on which this statement is based are as

yet unpublished). Some of these species have succeeded in crossing the Nile-Congo divide and some occur even in the Niger system, but have not entered Lake Victoria. As some of these species are apparently restricted to certain host genera such as *Lates*, *Hydrocyon*, *Citharhinus* etc. whose entry into Lake Victoria has been barred by the Murchison Falls an explanation of their absence is not far to seek.

At least five species are now known from the Malagarasi River and swamps, whose headwaters arise only a few miles from the Lake Victoria drainage area, which are also apparently absent from the lake. As three of these are apparently capable of parasitising any mormyrid fish, and as mormyrids are plentiful in Lake Victoria, it appears that transmigration in this region has not been easy.

One as yet undescribed species from the Tana system, Kenya, is also unrecorded from Lake Victoria.

The general picture presented, therefore, is that of a lake which shows evidence of a considerable degree of isolation from adjacent drainage areas, but which has been isolated for an insufficiently long period of time to permit the development of many (perhaps any) endemic species.

SUMMARY

An account is given of the parasitic Crustacea of Lake Victoria and the Victoria Nile. Seven species of Copepoda, of which three are new, and three species of Branchiura, of which one is new, are described, and the presence of the copepod *Lernaea cyprinacea*, unknown elsewhere in Africa, is recorded.

Biological data, including information on the development of certain species, are given, and the comparative ecology of *Argulus africanus* and *Dolops ranarum* is discussed.

The geographical distribution of the species recorded is briefly discussed and the impoverished nature of Lake Victoria when compared with the rest of the Nile system is pointed out. The parasitic crustacean fauna of the lake is indicative of a period of isolation, but one of insufficient duration to permit much speciation.

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LARVAL DEVELOPMENT IN THE GENUS *CHONOPELTIS* (CRUSTACEA : BRANCHIURA)

BY

GEOFFREY FRYER

*East African Fisheries Research Organisation, Jinja, Uganda**

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(With 7 figures in the text)

A description is given of the larval development of *Chonopeltis brevis* and of a species of which the adult is not yet known. All stages of development are parasitic on fishes, and different hosts are employed by larvae and adults. Attachment is described and host transfer is discussed.

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INTRODUCTION

Hitherto larval development in the branchiuran genus *Chonopeltis* has been scarcely known. The first fragmentary information was provided by Barnard (1955) who gave brief notes and sketches of what prove to be late-stage larvae of a species whose specific status is uncertain (Fryer 1960). Shortly afterwards a description of the structure and some of the habits of newly-hatched larvae of *C. inermis* Thiele was given (Fryer 1956) but, for reasons now apparent, it was not found possible to rear these larvae. These first-stage larvae differ not only from both the types of larvae which occur in the genus *Argulus* and from the larva of *Dolops* (to be described in a subsequent publication) but also exhibit features which are apparently unique among crustacean larvae. As a result of the kind co-operation of fellow workers it is now possible to give an account of their subsequent development and to explain some of the hitherto puzzling features of the earliest stages.

Larval stages of two species have now been studied. Both have been found to be parasitic on fishes from the earliest stages, and, although they occur in widely separated parts of Africa, both have been found to utilise as hosts members of the same genus—*Amphilius*—though one species at least is not

* Present address :— Freshwater Biological Association, The Ferry House, Far Sawrey, Ambleside, Westmorland.

exclusively confined to it. In one case it is known with certainty that the larval host does not serve as host to the adult and it is presumed with good reason that this applies in the case of the other species. In all cases the larvae have been found attached either to the inner wall of the operculum or to the pectoral and pelvic fins and their bases by means of the maxillules (which are referred to as maxillae in many accounts of the Branchiura) in a manner which varies according to the stage of development and which is described below.

ANATOMY OF THE LARVAL STAGES

The material studied consisted of a fairly complete series of larvae of *C. brevis* Fryer taken from *Amphilius grandis* Boulenger and *Garra* sp. in the Ragati River, a tributary of the Tana River, in Kenya by Mr P. J. P. Whitehead; a similar series of specimens of the same species taken from *Amphilius* sp. in the upper reaches of the Mugambuzi River (which flows into the north-eastern part of L. Tanganyika) Tanganyika Territory, collected by Mr D. Eccles; and a series of specimens of a distinctly different species collected from *A. grammatophorus* Pellegrin and *A. rheophilus* Daget by Dr J. Daget, in the Konkoure and Mamou Rivers, Guinea, West Africa, which are situated to the South-west of Fouta Dialon and flow into Sierra Leone. For convenience the larvae of *C. brevis*, whose eggs have been illustrated elsewhere (Fryer 1961), are described first and in greatest detail and notes on the West African larvae are given in a comparative manner later. Most of the morphological details are illustrated by figures thereby eliminating tedious descriptions. The numbers given to all but the earliest stages are somewhat arbitrary as certain instars appear to be unrepresented in the available material and it is not always certain how many of these are missing. Stage numbers, therefore, are used as convenient labels rather than as a precise indication of the number of moults involved.

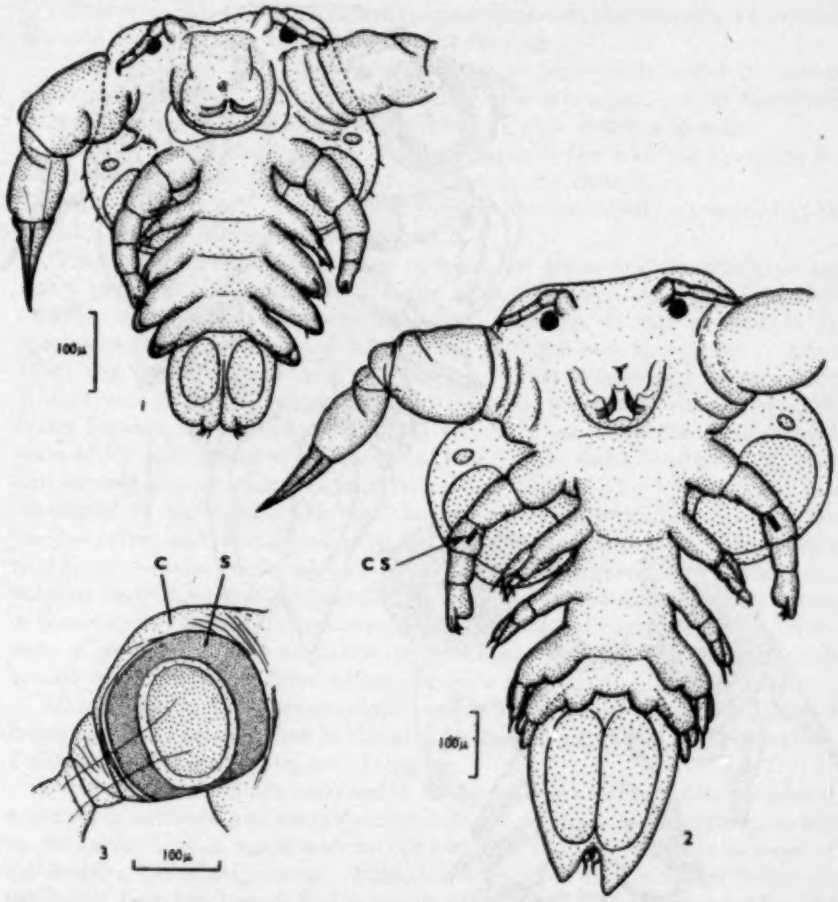
Chonopeltis brevis

Stage 1 : That parasitism commences at the earliest stage of larval development is shown by the presence, *in situ* on the host, of Stage 1 larvae from the Mugambuzi River, and by larvae, presumed by comparison to be of the same stage, in the West African material. Larvae of *C. brevis* at this stage correspond in almost all respects with newly-hatched larvae of *C. inermis*, which have been described and illustrated elsewhere (Fryer 1956), and are of similar size (Length c. 405μ). In the larvae of *C. inermis* a pair of minute chitinous spinules is found between the antennae. These were thought to represent the rudimentary antennules, but as they have never been seen in *C. brevis* it would seem that they are mere ornamentations and should not be looked upon as rudiments or relics of antennules.

Segmentation of the antennae is more clear in this and the next stage of development than in the later stages.

Stage 2 : (Fig. 1). The only changes apparent, other than an overall increase in length to about 520μ, are an increase in length of the abdomen, a slight development of setae on some of the legs, and an increase in the number of segments of the maxilla from four to five.

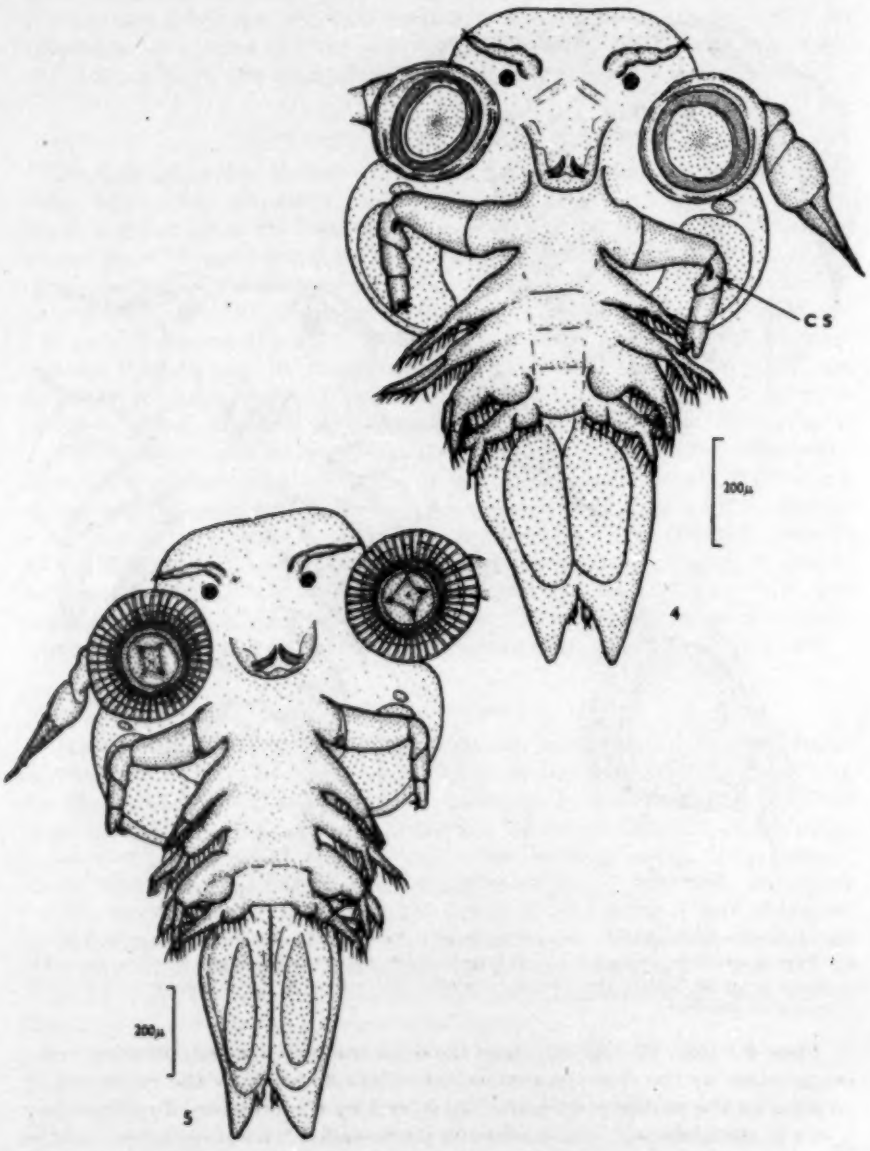
Stage 3 : It is certain that one, and possibly two, stages exist between Stage 2 and that next available. Their absence offers no serious obstacle in the tracing of development.



Figs. 1–3—*Chonopeltis brevis*. 1.—Larva, stage 2. Ventral. 2.—Larva, stage 4, male. Ventral. 3.—Base of maxillule, ventral, of a stage 4 larva which is about to moult and in which the sucker rudiment is visible beneath the cuticle. Legend :—C. Cuticle ; S. Sucker rudiment ; CS. Comb of setules on maxilla.

Stage 4 : (Fig. 2). At this stage the sexes can be separated, the male being recognisable by the close approximation of legs 3 and 4, by the rudiments of pouches on the posterior margin of leg 3, and by the presence of rudimentary testes in the abdomen. In the female the so-called " natatory lobes " of the fourth pair of legs are more conspicuous than is the case in the males. The general structure of a male at this stage is evident from Fig. 2. A comb of

very fine setules is present on segment three of the maxilla at this and certain later stages but it is not found in the adult. Its functional significance is not apparent.



Figs. 4–5—*C. brevis*. 4.—Larva, stage 6. Male. Ventral. 5.—Larva, stage 8, Male. Ventral. Cs. Comb of setules on maxilla.

At this stage it is possible, in specimens which are about to moult, to observe in the swollen basal region of the maxillule (segmentation is obscure at this stage) the sucker Anlage (Fig. 3) which takes the form of a thickened ring of tissue with an inner rim of presumably chitinous material.

Stage 5 : It is possible that a stage exists between that described above and the one described below, but this has not been seen.

Stage 6 : (Fig. 4). The sucker Anlagen are now quite apparent but are still non-functional. Leg setation is fairly well developed and the beginnings of modification of legs 3 and 4 in the male are now clearly apparent.

Stage 7 : This stage is very similar in general facies to the foregoing but the rudiments of supporting ribs are present in the suckers.

Stage 8 : (Fig. 5). The ribs of the sucker are now clearly apparent but the larval " hooks " of the maxillule remain.

There may be one further stage between the above and the adult, for one badly preserved male somewhat larger than the preceding seemed to show atrophy of the maxillulary hooks. Size, however, is rather variable for specimens at a given stage of development as is the case in *Argulus* (Tokioka 1936) and the atrophy noticed may have been due to imperfect preservation. It does seem probable, however, that at least one stage, either larval or adult, exists between the one ascribed tentatively to stage 8 and the earliest adult male which still remained on the larval host. This had a length of 2·01 mm. and superficially at least was fully developed, though whether the testis was functional is uncertain. The most important changes taking place between the last larval and the earliest adult stage are the complete loss of maxillulary hooks, an increase in the size of the suckers, the development of chitinous anterior supporting rods in the headshield, and the completion of differentiation of the accessory sexual apparatus on legs 2, 3 and 4 of the male. The modifications of leg 2 are, at this stage, not quite so accentuated as in larger males but specific identification is nevertheless possible.

If, as seems likely, there are eight or nine larval stages then the number of larval instars is greater than is the case in *Argulus japonicus* Thiele in which Tokioka (1936) found seven larval stages.

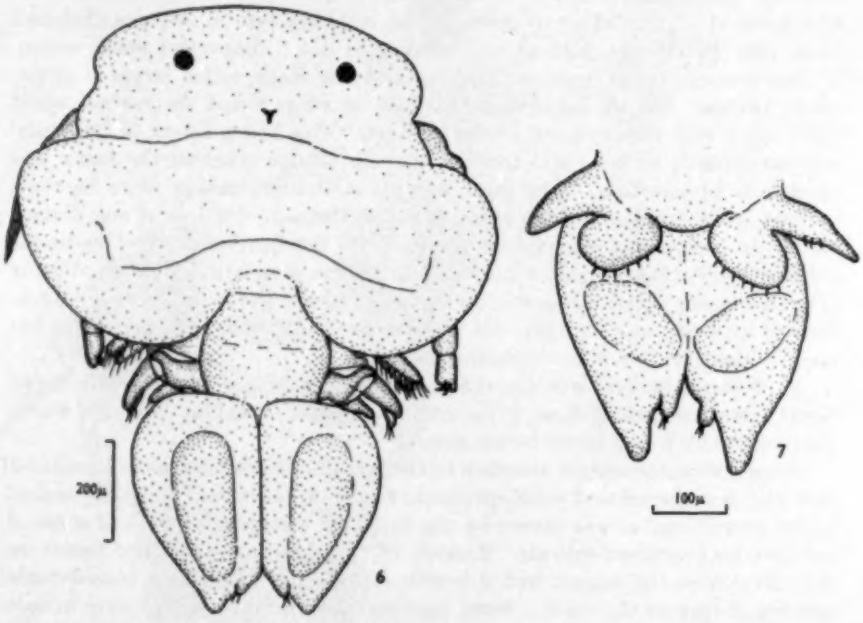
Some specimens remain attached to the larval host until complete structural maturity is achieved and some specimens found on *Garra* had definitely mated on the larval host as was shown by the fact that the spermathecae of some of the females contained sperms. Indeed, of the three adult females found on the larval host the largest had a length of 3·88 mm and had a considerable number of eggs in the uteri. Some eggs (capable of being laid ?) were in fact present in the uteri of even the smallest adult female which was 2·52 mm. in length.

Throughout larval development, but less noticeably so in the earliest stages, the larvae are pigmented dorsally. The pigment is brown in colour and is distributed in the form of small spots over much of the carapace, thorax and abdomen. Pigmentation is usually, but not invariably, darker in the specimens from the Mugambuzi River than in those from the Tana system. In the young adult females the general pigmentation gives way to the two bands of black pigment overlying the uteri which are so marked a feature of the adult females of this species.

The chitinous supporting rods of the anterior part of the carapace head-shield complex which are a noteworthy feature of the adults of all described species of *Chonopeltis* save *C. flaccifrons* Fryer, are not present in the larval instars. This suggests that in *C. flaccifrons* their absence is to be interpreted as a neotenic feature.

The larvae from West Africa

These larvae cannot be given a specific name at present as the adult is unknown, and in fact no member of the genus is known in the adult state from West Africa. From what is known of the geographical distribution of the genus, and from their structure, it seems probable that they are larvae of an undescribed species. Certainly they are specifically distinct from the larvae of *C. brevis* and *C. inermis*, and it is unfortunate that the most mature male (Fig. 6) is at a stage of development which is removed from the adult condition by one, or at the most two, moults.



Figs. 6–7—Larvae of an unknown species of *Chonopeltis* from West Africa. 6—Larva, stage 8. Male. Dorsal. 7—Fourth pair of legs and abdomen of larva, stage 7. Female. Ventral.

The earliest larvae present are, almost certainly, Stage 1 larvae, and are in fact smaller than the first stage larvae of either *C. brevis* or *C. inermis*. Their length is about 390μ. Throughout development the larvae are a little smaller than comparable stages in *C. brevis*. In the most mature male available some of the modifications of leg 4 are visible beneath the cuticle (Fig. 6). The most mature female is at Stage 7 and indicates that the adult of this species will

have large " natatory lobes " on the fourth pair of legs (Fig. 7). In all, and more particularly the later, stages dark brown pigmentation is present dorsally as is the case in *C. brevis*.

ATTACHMENT OF THE LARVAE

As a result of the finding of larvae *in situ* on the host the function of the chelate larval maxillules is now apparent. These appendages, which in essentials are constant in structure throughout larval life, are used to anchor the larvae to the surface of the host. The smallest larvae observed *in situ* were invariably attached by one maxillule only, the whole of the body being as it were pivoted about the appendage. In a few cases more advanced larvae were attached by both maxillules, but even here attachment by a single appendage was the most common method observed. Attachment is effected by plunging the barbed tip of the two opposed spines into the superficial layer of mucus and skin of the host. The significance of the sliding movements of the two spines observed in newly hatched larvae of *C. inermis* (Fryer 1956) is now apparent. Initial attachment and the forcing of the barbed tips of the two spines of the maxillules into the host tissue, is presumably achieved by means of the hooked antennae and maxillae. As soon as this is accomplished sliding movements will successively force first one then the other ramus a little further into the host tissue until the tip, which then functions as a single unit, is driven to a sufficient depth to serve as an efficient anchor. A glance at Fig. 78 in the paper in which the larva of *C. inermis* is described makes this clear. These spines are obviously specialised derivatives of simple hooks such as occur on the larval maxillule of species of *Argulus*.

It is not yet clear what happens at times of ecdysis. One might have expected to find cast cuticles still attached to the host, but this is not the case, so it may be that when the unattached maxillule is freed from the old cuticle it is inserted into the host and its partner is pulled free (though the barbs must make this rather difficult) before its cuticle is shed.

The suckers develop on the ventral face of the maxillules and are therefore closely opposed to the surface of the host from the time of their inception. As they become functional they replace the spines as organs of attachment.

Several larvae often occur in close proximity to each other, as many as eight, at various stages of development, having been found beneath a single operculum.

THE ENIGMA OF HOST TRANSFER

The reason why a host different from that parasitized by the adult is utilised by the larvae of *Chonopeltis* is obscure, and in fact adds to the already considerable difficulty of understanding how the parasite manages to perpetuate itself. Neither the adult nor the larvae are capable of swimming, so such dispersal as takes place must be essentially passive. Observations on attempts at mating in C. *shoutedeni* Brian (Fryer 1959) suggests that both participants may leave the host at this time, and all the facts so far available indicate that the eggs are laid away from the host. This means that if egg-laying is to take place

more than once the adult must locate a host for a second time. It is difficult to understand how this could be accomplished.

Amphilius and *Garra* are bottom-dwelling fishes, and it is not difficult to imagine that, particularly if the preferred habitat for egg-laying of *Chonopeltis* approximates to that frequented at times by these fishes, chance encounters between them and *Chonopeltis* larvae, which presumably use their clawed appendages for temporary attachment to the bottom, are not infrequent. Opportunities may therefore be greater at this stage for attachment to *Amphilius* and *Garra* than to the definitive host—species of *Labeo* and *Barbus* in the case of *C. brevis*. The size of the host may also be important for *Amphilius* and *Garra* are much smaller fishes than those which serve as hosts to the adult both of *C. brevis* and of other species. How attachment is initiated is unknown, but it seems probable that the tiny larvae either enter via the mouth and hook themselves to the operculum as they leave the oral cavity with the exhalent respiratory current, or hook themselves to the ventrally located fins as the host fishes pass over them. Size alone may be sufficient to cause the young adults to vacate the intermediate host, for space beneath the operculum and on the fins of *Amphilius* and *Garra* is restricted. Direct transference from the larval to the definitive host seems improbable so it can only be assumed that by the time the parasite reaches the size at which it leaves the intermediate host it is more suitably equipped for locating the definitive host. It is probably significant that the fishes which serve as definitive hosts to all known species of *Chonopeltis* are, without exception, bottom feeders, and this suggests that the parasite attaches itself to the bottom, awaits the arrival of a host and, possibly by the utilisation of some as yet unobserved mechanism, contrives to attach itself.

Parasites may very occasionally leave the intermediate host before they have completed the larval stages, for on one occasion a late larva of *C. brevis* (Stage 8) was taken from a specimen of *Barbus altianalis radcliffi* Boulenger, the definitive host, in the Victoria Nile (Fryer 1961). That this is a rare occurrence is shown by the fact that, of several hundred specimens of six species of *Chonopeltis* collected by the writer from their definitive hosts, this is the only larval specimen encountered. It is suggested that *Synodontis*, from which Barnard (1955) collected three immature specimens of a *Chonopeltis* in the Okavango River, is an intermediate and not a definitive host.

SUMMARY

An account is given for the first time of larval development in the African branchiuran genus *Chonopeltis*. Information is given on *C. brevis* and on a species of which the adult is not yet known.

Newly hatched larvae, whose structure is unique within the Crustacea, attach themselves, in the case of both the species studied, to the inner surface of the operculum or to the pectoral and pelvic fins and their bases of small catfishes of the genus *Amphilius* and small cyprinids of the genus *Garra*, both of which are riverine in habits, by means of highly specialised maxillules whose structure and mode of action are described.

Amphilius and *Garra* serve as hosts only to the larvae. The adults in one case parasitise large cyprinid fishes of the genera *Barbus* and *Labeo*. The

host of the adult of the other species is not known. Development proceeds gradually during which, as in *Argulus*, suckers gradually develop in the basal regions of the maxillules. Various stages of development are illustrated. The exact number of larval stages had not been ascertained, but it seems likely that eight or nine are involved.

Problems concerning the means whereby the larvae, and subsequently the adults, locate and attach themselves to host fishes are discussed. These problems are particularly intriguing as neither larvae nor adults are capable of swimming.

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SOME OBSERVATIONS ON THE LIFE HISTORY OF *ASELLUS AQUATICUS* (L.) AND *ASELLUS MERIDIANUS* RACOVITZA (CRUSTACEA : ISOPODA)

BY

E. A. STEEL

Department of Zoology, Reading University *

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(With 4 figures in the text)

The object of this research was to discover details of the life history and breeding biology of the two species of *Asellus* found in the surface waters of the British Isles. Data were obtained from monthly samples taken from two habitats. Analysis revealed that the species are similar in most aspects that were investigated but that the life histories show slight differences in timing.

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INTRODUCTION

There are two species of fresh-water isopod in the surface waters of the British Isles, *Asellus aquaticus* (L.) and *Asellus meridianus* Racovitza. The object of this work was to compare the life histories and general biology of the two species.

Until 1919 the name *Asellus aquaticus* covered all the fresh-water isopods found in this country and on the Continent. Racovitza (1919) after studying

* Present address : Field Station for the Study of Animal Behaviour, Department of Zoology, Cambridge.

A. aquaticus from France, England and various other localities, distinguished two species, and gave full descriptions and illustrations of each. Racovitza retained *A. aquaticus* for the isopod most common in Northern Europe. The other he named *Asellus meridianus*. Later Dudich (1925) reviewing the taxonomy of the group created a new subgenus ; he retained the name *Asellus* (*sensu stricto*) for *Asellus aquaticus*, but placed *A. meridianus* in a new subgenus *Pro-asellus*.

Soon after the naming of the new species *A. meridianus* it was recorded in various parts of England (e.g. Derbyshire, Tattersall (1920) ; Kent, Chilton (1920)). Subsequently this species has been found to be widely distributed over the country.

Two obvious morphological differences between the two species useful for identification in the field have been noted. Scourfield (1940) recorded that the dorsal median area of the head capsule in *A. aquaticus* is devoid of pigment, while in *A. meridianus* there are two lateral unpigmented areas. Lockwood (1959) found differences in the distribution of urate cells forming Zenker's organ. This character can easily be seen through the cuticle of an intact animal.

Little has been written on the ecology, behaviour or life history of *Asellus*. Omer-Cooper (1925) recorded the two species from Wicken Fen, *A. meridianus* being the more abundant. Both species also occur in the Lake District where Moon (1957 a) came to the conclusion that *A. aquaticus* has been introduced by human agency into Lake Windermere and that it is competing with the indigenous *A. meridianus* in the littoral zone ; the latter is now only maintaining itself successfully below a depth of two metres. In a survey of the distribution of *Asellus* in the Lake District and adjoining areas, Moon (1957 b) found no correlation with any known physical or chemical factor.

Reynoldson (in press) has been able to correlate the presence or absence of *Asellus* in lakes with the amount of calcium and total dissolved matter (T.D.M.) in the water by an analysis of his own and Moon's data. At low levels of calcium and T.D.M. *Asellus* is usually absent while high levels are generally favourable to it. In between is a marginal zone where *Asellus* is present in about 50 per cent of the lakes examined, and where its distribution may be affected by altitude.

Recent papers on the distribution of *Asellus* in Western France and Scotland have been published by Hynes (1959) and Warwick (1959). These give no indication of habitat differences between the two species.

METHODS

General

The life history of each species was studied by taking monthly samples from two habitats. Samples of *A. aquaticus* were taken from a bed of *Acorus* in the River Thames (Nat. Grid. ref. 41/757748), and samples of *A. meridianus* were taken from a small enclosed pond in oak woodland (Nat. Grid. ref. 41/581699). Originally it was hoped to collect from a still-water and a running-water habitat for each species, but in the area covered (i.e. the Reading area)

A. aquaticus was not found in true pond conditions or *A. meridianus* in running-water. Sampling was begun in October 1958 and continued for fourteen months.

Collecting

Collecting methods were varied to fit best the type of habitat. All material was brought back to the laboratory for sorting.

Thames. Decaying vegetation containing *Asellus* was pulled out of the river by hand. Occasionally *Asellus* was collected off rotting logs. As no particular size-group sought shelter on the logs these animals were put with the general collection.

Chapel Row Pond. *Asellus* was living on the surface of oak-leaf litter down to a depth of one to two inches. Collections were made by skimming off the top layer of leaves with a square sided pond net.

Sorting

The collected vegetation was taken to the laboratory in buckets of water. The amount collected from each habitat was the same each month. The vegetation was put in sieves having eight meshes per inch. Tap water was played on this and the material stirred round to remove the mud. The muddy water was searched for any *Asellus* that had come through the sieve. The washed vegetation from all samples was then examined in white enamel trays and all *Asellus* seen were picked out.

A re-examination of material sorted in this way showed that at least 98 per cent of the animals were removed in a single operation.

Measurements

The live *Asellus* in a natural position tends to arch its body antero-posteriorly (with the dorsal side convex) and therefore cannot be measured from above with an eye-piece micrometer. To overcome this difficulty each animal was laid on its back so that the dorsal surface touched the substratum along the whole length. It was then superimposed on millimetre graph paper, mounted on a slide, and measured under a low power binocular microscope. The mid-front of the cephalon cannot be seen from below so the lateral angles were taken as the anterior end of the body, and the mid-point of the end of the abdomen as the posterior limit. Measurements were taken to the nearest 0·5 mm. below.

Presentation

The results were plotted as length-frequency histograms, each size group being expressed as a percentage of the total sample. The animals were sorted into half-millimetre size groups. All animals over 3 mm. in length were separated according to sex (Figs. 1 and 2). The life histories of the two species were deduced from these figures. It was assumed that within the collecting areas there was no differential habitat selection for different groups within the population. Sample size varied from 42 (April) to 1008 (July) in *A. aquaticus* and from 65 (May) to 415 (June) in *A. meridianus*.

RESULTS AND DISCUSSION

Life histories

Asellus aquaticus

The October 1958 to February 1959 samples show approximately normal distributions (Fig. 1). Throughout the winter the curve flattens out and the mode moves from 6 to 8 mm., but there is a large number of animals in the 6·5–7 mm. range which represents the October peak of 6 mm. which has spread out due to the differential growth of its members. The peak appears at 8 mm. in December and February (there is no January sample) and probably indicates that there is little growth during the coldest months. After February this peak can no longer be traced. The upper portion of the curve gradually disappears due to the death of the older, larger members of the population. Animals up to 12–13 mm. are present from December to April, but from June onwards none is found above 9 mm.

In February the breeding season begins ; ovigerous females appear in the sample. The older females are the first to breed and in this month range from 6–8 mm. As the season progresses more females breed and younger females are recruited into the breeding population (Table 1). The smallest breeding

Table 1—The size in millimetres of the smallest breeding female and numbers of ovigerous females and animals in pre-copula occurring in each month from February to October.

Month	Smallest breeding female		Ovigerous females as percentage total females		No. animals in pre-copula as percentage total population	
	A.aq.	*A.m.*	*A.aq.*	*A.m.*	*A.aq.*	*A.m.*
1959						
February	6·0		11	9	5·5	6
March	6·0	4·5	49	41	8·5	42
April	5·5	4·0	67	85	14	5
May	5·0	4·0	44	54	4	3
June	4·0	3·0	54	0	10	0·5
July	4·0	3·0	30	48	8	16
August	3·5	3·5	38	43	8	
September	3·5	3·0	58	51	12	
October			5	7		

female is 6 mm. in February and March, but at the end of the summer animals only 3·5 mm. are breeding. Sexual maturity in those animals born at the beginning of the summer, is reached at a length of 3–4 mm. while the autumn born ones grow slowly through the winter and have attained a length of a least 5 mm. before they breed the following spring.

The peak of breeding is reached in April, two months after the start of the season when nearly 70 per cent of the females are carrying eggs. After this there is a gradual decline throughout the summer until September when a secondary peak occurs. This recrudescence of breeding is quickly terminated in the autumn. A few ovigerous females remain in October but by November all the females have released their young and no more eggs are laid. Although

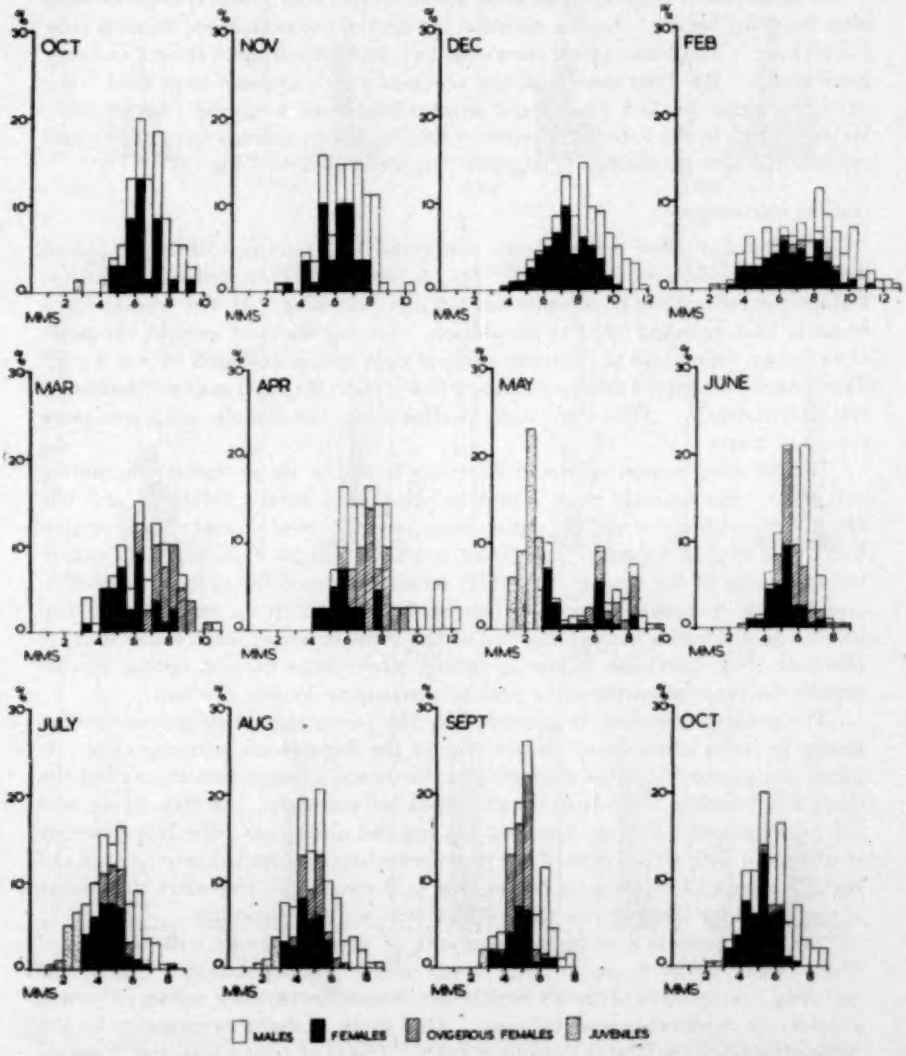

Fig. 1—Length-frequency histograms of *Asellus aquaticus*. Each size group expressed as a percentage of the total sample.

the percentage of ovigerous females varies from month to month there is effectively one breeding season lasting from February to October. The number of ovigerous females as a percentage of total females during this time never drops below about 30 per cent. There are, however, two definite peaks within this season when the percentage rises to 67 per cent and 58 per cent in April and September respectively.

No members of the 1959 generation are seen until May ; that is three months after breeding begins. In this month 6 per cent of the sample are animals only 1 mm. long. The May sample shows the two distinct curves of the old and new generations. By June nearly all the previous year's animals have died ; the curve is single peaked again, and approximates to a normal distribution. Rapid growth in the first two months of life brings the animals to maturity and in June the new generation is beginning to breed (§4F and Fig. 4).

Asellus meridianus

The October 1958 curve shows a normal distribution with about equal numbers of males and females (Fig. 2). A few females are still carrying eggs. Fifteen per cent of the population are 1–3 mm., showing that new animals have recently been released into the population. During the next months the mode remains at 4 mm. and the largest animals only reach a length of 8–8·5 mm. The peak moves from 4 mm. in February to 6 mm. in May and may well represent the same animals. After this young *Asellus* dilute the sample and a new peak occurs at 2 mm.

The breeding season begins in February with the larger females becoming ovigerous. No animals were found in pre-copula before February and the first ovigerous females had eggs at an early stage of development. The sample was taken in mid-February and it seems likely that no eggs were laid before the beginning of the month. The first females to breed range from 5–6·5 mm. and as with *A. aquaticus*, smaller females breed later in the summer. It can be seen that females born at the end of the summer are at least 4 mm. long by the time they breed the following spring, while those born in spring mature rapidly and can breed the same year at a minimum length of 3 mm.

The peak of breeding as measured by the percentage of ovigerous females comes in April when about 85 per cent of the females are carrying eggs. It takes two months from the beginning of the season to reach this climax but the decline in breeding after April is more rapid and complete. In May 50 per cent are ovigerous, and in June breeding has stopped altogether. In July breeding starts again with 40 per cent of the new generation females being ovigerous and reaches a peak of little under 50 per cent in September. Hereafter the decline is rapid and by October less than 10 per cent are still breeding.

In June there is a sudden appearance of young animals with a mode of 2 mm., those under 3 mm. forming 68 per cent of the population. The second breeding season from July to September results in another influx of young animals in September and October. This gives a slight asymmetry to the population curve as late as December 1959. The peak is at 4 mm. but there are more animals below this size than above it ; more animals of 2·5 mm. and 3 mm. are present than in the preceeding year. It looks as if the late breeding

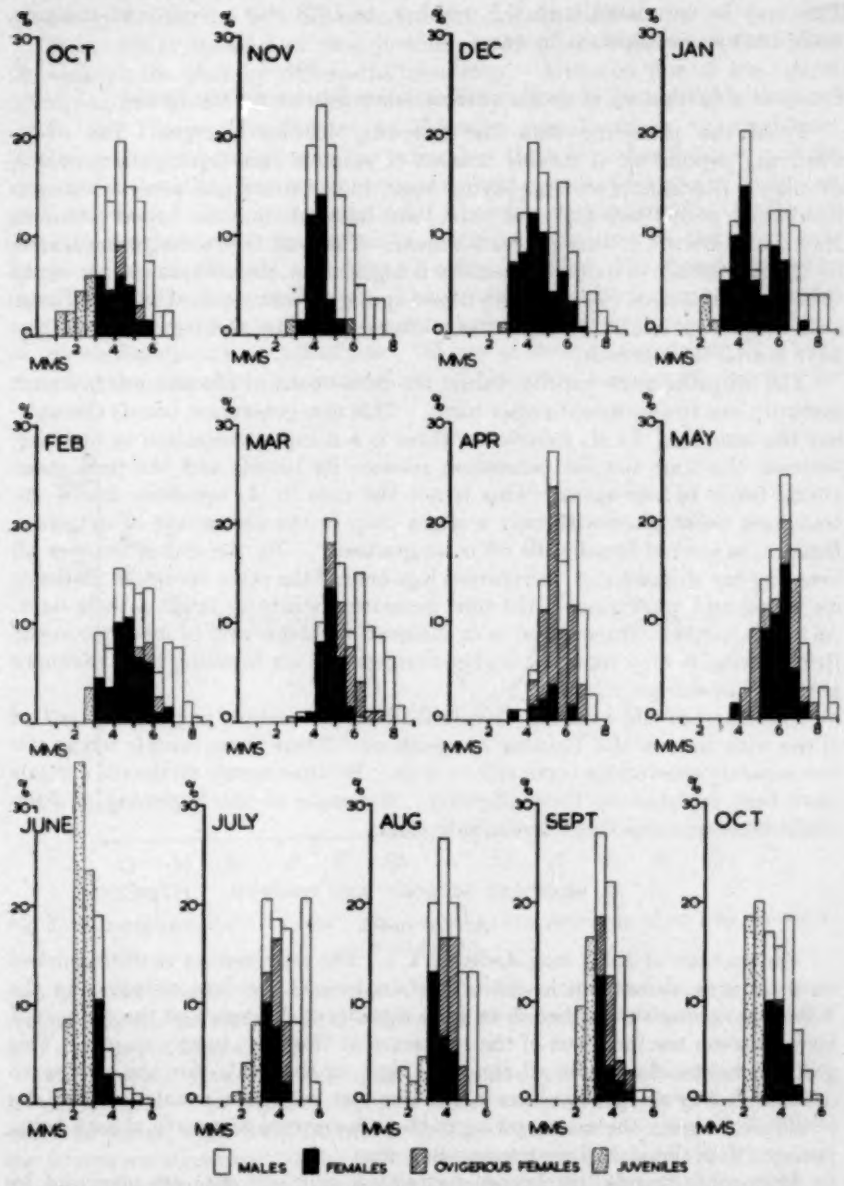

Fig. 2—Length-frequency histograms of *Asellus meridianus*. Each size group expressed as a percentage of the total sample.

season was more successful and lasted longer in 1959 than in the previous year. This may be correlated with the weather, as 1958 was a very cold summer while 1959 was exceptionally warm.

Synopsis of life history of Asellus and variation between the two species.

From the preceding data the following picture emerges. The over-wintering population of *Asellus* consists of animals born during the previous summer. Copulation and egg-laying begin in February and after a variable incubation period (see §4B) the young are released from the brood-pouch in May (*A. aquaticus*) or June (*A. meridianus*). The peak of breeding as measured by the percentage of ovigerous females is higher in *A. meridianus* (85 per cent) than in *A. aquaticus* (67 per cent) whose spring breeding period is spread over a slightly longer time. Males die soon after copulation, and females after they have reared their broods.

The offspring grow rapidly during the first weeks of life and reach sexual maturity one to two months after birth. This new generation breeds throughout the summer. In *A. meridianus* there is a complete cessation in breeding between the time the old generation releases its broods and the time these young begin to reproduce. This is not the case in *A. aquaticus* where the transition takes place with only a slight drop in the percentage of ovigerous females, as the old females die off more gradually. By the end of October all breeding has stopped. *A. meridianus* lags behind the other species in releasing its young and consequently the new generation starts to breed a little later. As it is a southern species, and is at the most northern part of its range in the British Isles, it may require a higher temperature for breeding than the more northerly *aquaticus*.

The stage of life cycle in Chapel Row *A. meridianus* is probably out of phase with that in the Thames *A. aquaticus*. There is no sample where the two separate generations occur side by side. By June nearly all the old animals have been replaced by their offspring. A sample at the beginning of June might have revealed this intermediate stage.

4. BREEDING BIOLOGY AND GROWTH

A. *Sex ratios*

The sex ratio of 3 mm. long *Asellus* is 1 : 1. The sexes cannot be distinguished until the animals are this length. A χ^2 analysis of the data collected for the 3–3·5 mm. group shows that there is no significant difference at the 5 per cent level between the members of the two sexes at this size, in any month. This group consists of animals all the same age, as the peaks for the two sexes coincide. Any size group above 3 mm. however, will contain males and females of different ages ; the males, owing to their faster rate of growth always being younger than females of a corresponding size.

Monogenic broods (i.e. broods containing only one sex) are produced by *A. aquaticus* (Seitz 1953). This occurs also in other isopods (Howard 1939 and Vandel 1939) and is due not to parthenogenesis but to the consistent production by the female of eggs containing the X or Y chromosome. If monogeny does

occur in these populations it must either be very rare, or must be balanced in some way to give the 1 : 1 sex ratio found in young *Asellus*.

Seitz (1954) shows how this juvenile ratio of *A. aquaticus* is modified throughout the year by differential mortality. Although few of his figures are significant his deductions are confirmed by my data for both species.

In the Thames the October to February samples show no significant difference in numbers between the sexes, but there is a change from a slight excess of males in the first two months to a slight excess of females in December and February. This trend continued throughout the spring. In March (N=79) females far outnumber males, χ^2 being significant at the 1 per cent level. In April (N=42) and May (N=88), however, the figures are only significant at the 5 per cent level. This anomaly cannot be accounted for by recruitment of males into the sample, but there may be a small mortality among ovigerous females at this time of year. However, these figures clearly show that in spring the males having copulated die off before the females who survive for

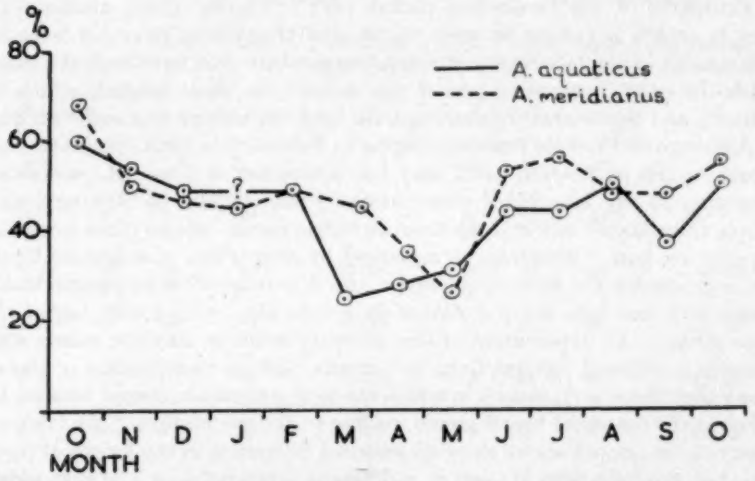

Fig. 3—Seasonal variation in sex ratio. Males expressed as a percentage of the total population over 3 mm.

two or three months longer to rear their broods. As the new generation in August reaches the size where the sexes can be determined, the basic sex ratio of 1 : 1 is again approached.

The Chapel Row samples show a similar pattern of sex ratios for *A. meridianus*. The October and November samples show a non-significant excess of males, while from December to May females predominate. In April the figures are significant at the 5 per cent level and in May at the 1 per cent level, showing that the male mortality increases until just before the peak in breeding. From June onwards the proportions are again approximately equal.

At Chapel Row the old generation was reduced to 6 per cent of the population by June. Although the young animals enter the sample one month earlier in

the Thames, the old generation disappears about the same time in each species. Its demise is, however, less catastrophic in *A. aquaticus* being spread over two months rather than one. This is shown in Fig. 3 in which the males are plotted as a percentage of the total population over 3 mm. If this curve is read upside down it shows the decline in the relative number of females. There is a very sharp drop between May and June in the *A. meridianus* curve, and a gradual one from March to June and July for *A. aquaticus*.

While the general pattern of seasonal mortality is the same in both species the rates at which the sexes die differ. The males of *A. aquaticus* die off rapidly in early spring while the female mortality begins a month or so later and is a more gradual process. With *A. meridianus* the reverse is seen. The decline of males lasts from February to May, while most of the females disappear between May and June.

B. *Length of incubation period*

Estimates of the incubation period vary ; Unwin (1920) quotes typical cases in which it ranges between thirty and thirty-four days. I have kept both species in the laboratory at room temperature, but have only six cases in which the exact incubation period was noted. In these animals which bred in March and September incubation took between sixteen and eighteen days.

Although in the field breeding begins in February in both species no young appear in the population until May (*A. aquaticus*) or June (*A. meridianus*). According to my laboratory observations young should be coming into the sample from March onwards, as they leave the parent two to three weeks after the eggs are laid. Breeding, as measured by proportion of ovigerous females, begins gradually and rises to a climax, and it is reasonable to assume that the release of young into the population should do also, with a time lag of about three weeks. An explanation of this anomaly could be that the young *Asellus* occupies a different habitat from its parents, but an examination of the data shows that there is no month in which the new generation cannot be seen to be either in the maternal brood-pouch, or free in the population. My laboratory observations quoted above show no seasonal difference in the length of incubation, but the field data is open to a different interpretation. If one adds the percentages of females breeding in the three months before the new generation appears, one finds that the total is well over 100 per cent.

Provided that mortality among ovigerous females is not substantially higher than among non-ovigerous ones this implies that females carry their eggs for an average period exceeding one month. Heeley (1941) found that the incubation period of some terrestrial isopods, which produced more than one brood per year, was longer for broods hatched at the beginning of the season than for those hatched later. With *Asellus* one can say that the incubation period in the field must be less than three months and exceed one month in duration. The period probably varies even among those animals breeding in the spring as in *A. meridianus* all eggs laid between February and May are released between mid-May and mid-June. This suggests a temperature or day length control rather than an internal clock set for spring breeding.

C. *Number of broods per female*

I can find no evidence that females produce more than one brood between February and October. Animals born in autumn breed the following spring and die after liberating their brood ; these young have time to breed only once before autumn. I have kept post-reproductive females in the laboratory with potent males, but although pre-copula is frequent and often prolonged, no broods were ever produced.

However, those born in spring breed in late summer and again in the following spring, thus breeding twice in their life-time. Their life span is probably longer than that of the previous group, that is, about twelve months as opposed to about nine months.

Table 2—Number of eggs per brood

Size group	*Asellus aquaticus*				*Asellus meridianus*			
mm.	N	mean	range	coefficient of variation	N	mean	range	coefficient of variation
3·0					6	11	9	
3·5					40	16	17	
4·0	27	21	30		32	20	25	
4·5	41	25	37	33·56	13	30	29	33·50
5·0	68	30	54	43·30	11	39	34	21·20
5·5	30	40	51	30·80	3	46	44	133·40
6·0	18	43	79	50·00	5	55	39	114·10
6·5	5	53	66		2	57	9	
7·0	10	100	71		1	99		
7·5	9	80	95					
8·0	14	98	175					
8·5	8	98	83					
9·0	8	106	103					
9·5	2	116	65					
10·0	3	147	59					

D. *Size of the brood*

There is great individual variation in the size of the brood produced by each species of *Asellus*. The mean brood size varies with the size of the female (Table 2). The range within each size group is large. In the 5 mm. group for *A. aquaticus* the mean value is 30, but any number from 7–61 may be found in an individual brood-pouch. The absolute range in *A. meridianus* is slightly less but still marked. The coefficient of variation indicates that the brood size in *A. meridianus* is more variable among smaller females, and less variable among larger females, than that of *A. aquaticus*.

A differential rate of reproduction could influence the relative members of the closely related species living in the same habitat. The data were analysed to see if female *Asellus* of the same size but of different species produce, on the average, broods of different sizes. The size overlap of breeding females of the two species includes animals between 4–7 mm. In all cases the mean number of eggs per brood was greater in *A. meridianus* than in *A. aquaticus*. The results of a t test applied to these data is shown below : —

Size Group	Number in sample		Value of t
	A. aq.	*A. mer.*	
4·5–5·0 mm.	41	13	1·86
5·0–5·5 "	68	11	1·78
5·5–6·0 "	30	3	Sample too small for analysis.
6·0–7·5 "	18	5	do.
6·5–7·0 "	5	2	0·01

This indicates that there is no significant difference between the mean brood sizes of the two species.

E. *Mortality during incubation*

Janke (1924) suggested that eggs and embryos are lost from the brood-pouch during incubation, his argument being that the marsupium is initially packed with eggs which would have no room to grow and develop unless some were expelled. The young at first feed on yolk provided by the egg and so do not actually increase in mass, but they take up more room as they change shape and develop appendages. During the larval stage they feed on detritus brought in with the ventilation current. To support this view Janke points out that the later embryos are not in any way constricted, as would be the case if all the eggs developed to this stage. He also claims to have watched eggs being passed out of the brood-pouch.

In an experiment to test this theory the developmental stages of *Asellus* were assigned to three arbitrary groups :

(i) eggs
(ii) early embryos
(iii) late embryos.

Eggs were so called from the time of laying through the initial process of cell division to the beginning of elongation. As soon as these lost their spherical

shape they were known as early embryos. This stage lasted until the first six pairs of thoracic appendages were present. From this stage to the time of release they were referred to as late embryos.

A number of counts were made of the brood-pouch contents of female *A. aquaticus* and *A. meridianus*, and the embryos referred to one of these three categories. To limit the variable which occurs as a result of the size of the parent influencing the size of the brood the parent animals were separated into 0·5 mm. size groups. The significance of differences between various groups was tested by t tests ; the results are shown in Tables 3 and 4.

Table 3—Comparison between mean numbers of eggs and embryos for *A. aquaticus* and *A. meridianus*.

	Size group	No. of animals with		Mean		Standard deviation		Diff. between mean nos. of eggs & embryos
	mm.	eggs	embryos	eggs	embryos	eggs	embryos	
Asellus aquaticus	4·5–5·0	42	27	39·5	23·25	13·92	9·32	16·32
	5·0–5·5	23	18	24·39	21·94	9·73	7·39	2·45
	5·5–6·0	16	13	45·50	31·61	11·47	9·04	13·89
Asellus meridianus	3·5–4·0	20	20	15·15	16·05	4·29	5·76	0·90
	4·0–4·5	17	16	19·58	18·81	4·55	9·98	0·77

Table 4—Comparison between mean numbers of early and late embryos for *A. aquaticus* and *A. meridianus*.

	Size group	No. of animals with :		mean		Standard deviation		Diff. between mean nos. of early and late embryos
	mm.	early embryos	late embryos	early embryos	late embryos	early embryos	late embryos	
Asellus aquaticus	4·5–5·0	9	9	18·88	20·55	9·14	7·72	1·67
	5·0–5·5	19	7	25·42	17·0	10·20	8·12	8·42
	5·5–6·0	(Sample too small for analysis)						
Asellus meridianus	3·5–4·0	10	10	15·2	16·9	4·66	7·04	1·70
	4·0–4·5	8	8	19·37	17·5	8·24	10·91	1·87

For *A. aquaticus* a comparison between the mean number of eggs and the mean number of embryos (early+late) from the brood-pouches of animals 4·5–6 mm. in length shows that these differences are significant at the 0·01 per

cent level. This suggests that numerous eggs are expelled during development, but does not indicate if they are expelled within a short period or whether there is a gradual reduction process lasting through the whole ovigerous period. The significance of the difference in average between early and late embryos was then tested. Only the two smallest size groups were used, as the third sample consisted almost entirely of early embryos. A reduction of numbers between the early and late embryo stages is only seen in the 5–5·5 mm. size group, and the difference is not significant.

The result from the analysis of the 4·0 mm. group shows, as in *A. aquaticus*, a reduction in the numbers from egg to embryo stage, but in this case it is small and not statistically significant. There is also a small drop in numbers between the two embryo stages. In the 3·5 mm. group the figures show an apparent rise in the number between the egg and early and late embryo stages. Clearly this is an impossibility and must be attributed to sampling errors.

From this it appears that greater numbers of young are lost during the egg stage in both species but this may be due to the fact that this stage lasts longer than the embryo stage. Therefore even a constant loss rate would give bias to the egg stage. The three stages chosen are entirely arbitrary and may have no relevence to the life of the animals.

The loss of brood indicated above was checked by keeping female *Asellus* in individual containers and examining the water daily for eggs expelled from the brood-pouch. Very few eggs were ever found free in the water. At best an animal lost two or three young over the whole developmental period. Also, contrary to Janke's belief, large numbers of embryos were seen tightly packed in one brood-pouch. One female was seen to release one hundred and sixty-six fully developed young. If a reduction in brood had occurred this would mean that an unusually high number of eggs was laid (Table 2).

Several explanations of the small number of eggs found free in the water suggest themselves. First, the parent might eat the egg soon after release. Secondly, cannibalism could occur in the brood-pouch. This could only occur during larval stage. Most eggs are lost before the young are capable of feeding. Last, the eggs could die and decay in the brood-pouch. Opaque, presumably dead eggs have been seen, but they are not common.

Janke reports that he saw eggs being expelled. If *Asellus* is disturbed by handling, or is placed on its back for observation of the brood-pouch, eggs are often expelled. The oostegites are withdrawn from the body and then forcibly closed down again several times in succession, and the eggs squeezed out.

The evidence from this data shows that some of the brood is lost during incubation, but the manner of this loss and its causes are unknown.

F. *Growth rates*

There is no size discrepency between males and females at the time of release from the brood-pouch ; they are all about 1 mm. length. This state lasts until the animals are 3 mm. long. This can be seen when the curve for each sex is plotted separately, as the 3 mm. peak for males and females occurs

in the same month. After this the males grow more rapidly and their peak of numbers is always in a larger size group than that of the females (Fig. 1 and 2). Fig. 4 shows the differential growth that takes place in the first month after the young *Asellus* come into the sample.

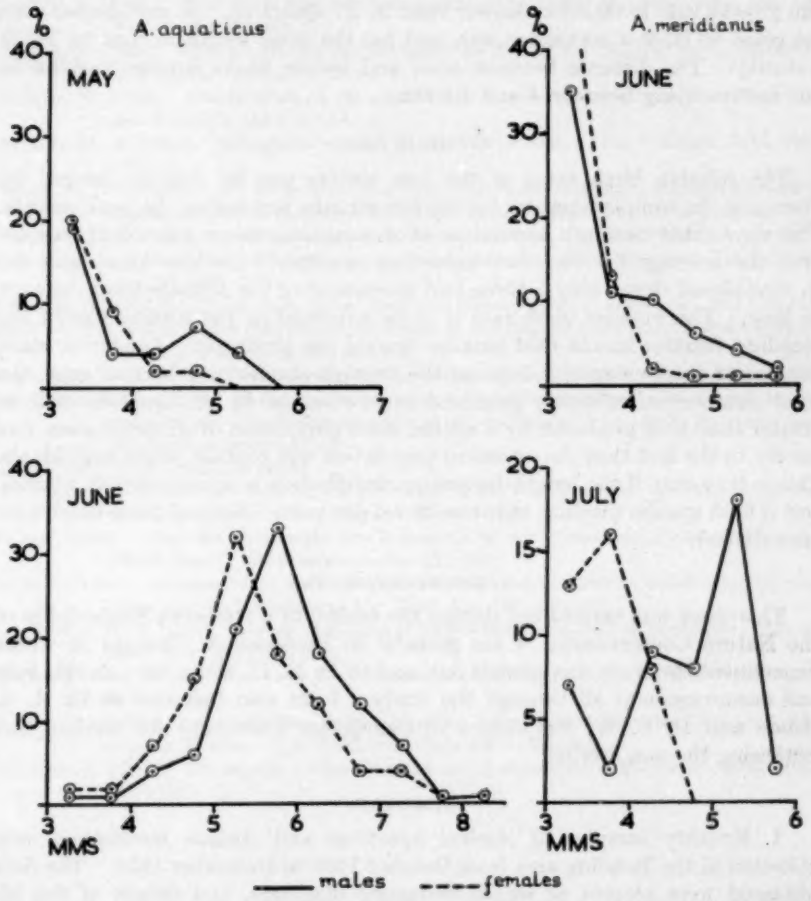

Fig. 4—Differential growth rates of young *Asellus* males expressed as percentage of total males ; females as percentage of total females.

A. aquaticus. In May the peak for young animals was at 2 mm. One month later these 2 mm. females had attained a length of 5 mm. and the males 6 mm. Thus the animals are capable of growing between 3 and 4 mm. in one month. It is not possible to trace these peaks with any certainty through succeeding months as the population curve is changed by more young animals coming into the sample, but the main bulk of males and females remain centred

about 6 mm. and 5 mm. respectively. In most samples throughout the year the peaks for males and females are separated by a gap of 1 mm.

A. meridianus. The young come into the sample later. The situation in June resembles that of *A. aquaticus* in May, with a peak of young *Asellus* at 2 mm. A month later in mid-July the females are 3·5 mm. and the males 5 mm. The growth rate is therefore slower than in *A. aquaticus*. *A. meridianus* does not reach so large a maximum size, and has the same length of time to reach maturity. The distance between male and female peaks is more variable in this species, lying between 1 and 1·5 mm.

G. *Birth rates*

The relative birth rates of the two species can be roughly gauged by averaging the sample numbers for the five months preceeding the peak sample. This shows that the July population of *A. aquaticus* shows a five-fold increase over the average for the five preceding months, while the June peak for *A. meridianus* shows only a three-fold increase over the average from January to May. This smaller birth rate is to be expected as the smaller size of the breeding females means that smaller broods are produced. As similar sized females of the two species bear on the average similar numbers of eggs, the total numbers of offspring produced in one season by *A. aquaticus* will be greater than that produced by a similar sized population of *A. meridianus*, due merely to the fact that the *aquaticus* population will contain larger individuals. This is true only if the length-frequency distribution is approximately normal, and if both species produce only one brood per year. Both of these conditions are satisfied.

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SUMMARY

1. Monthly samples of *Asellus aquaticus* and *Asellus meridianus* were collected in the Reading area from October 1958 to December 1959. The data obtained were plotted as length-frequency diagrams, and details of the life history and breeding biology were deduced from them.

2. The life histories are essentially similar in the two species, apart from small differences in timing.

3. The number of eggs produced by a female is directly proportional to her size ; similar size females of the two species produce on the average equal broods.

4. There is a wide variation in brood size for females of a given length. Small *A. meridianus* tend to be more variable than *A. aquaticus*.

5. It is inferred that some eggs are lost from the brood pouch during incubation, but direct evidence for this is not available.

6. The juvenile sex ratio is 1 : 1 but is modified throughout the year by differential mortality.

7. Some observations are made of growth rates and birth rates.

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TESTIS FOLLICLE NUMBER AND THE HIGHER SYSTEMATICS OF MIRIDAE (HEMIPTERA-HETEROPTERA)

BY

DENNIS LESTON

44 Abbey Road, London, N.W.8.

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(With 6 figures in the text)

Testis follicles of ninety-four mirid species are listed : subfamilies Phylinae, Dicyphinae, Orthotylinae and Mirinae have modalities of 3, 1, 2 and 7 respectively. Other features—pronotal collar, pretarsus, venation, genitalia, eggs and diploid numbers—are reviewed in the light of new information and a fresh grouping of subfamilies is suggested : Isometopinae ; Bryocorinae ; Mirinae + Deraeocorinae + ?Cylapinae ; Dicyphinae + Orthotylinae + Phylinae. The current tribal divisions in Orthotylinae are untenable and the distinction of this group from Phylinae is blurred. Membranous arolia have arisen twice in Miridae, the family originating from a nabid-like predatory ancestor. The two-celled membrane is more primitive than the one-celled, but retention of ocelli by Isometopinae is also a primitive feature. Species aberrent in follicle number include *Alloeotomus gothicus* and *Oncotylus viridiflavus* (indefinite follicle number) ; *Stenotus binotatus* and *Leptopterna spp* (additional follicles) ; *Notostira elongata*, *Orthocephalus coriaceus* and *Cyrtorhinus caricis* (departure from subfamily norm) : *Deraeocoris* is polyphyletic. Analysis of feeding habits has disclosed marked intersubfamilial differences.

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INTRODUCTION

Although Dufour (1833) described and figured the male reproductive system of Miridae—the capsid bugs of economic entomology—later morphologists tended to ignore the family, probably because of the difficulties determination of genera and species presents to the non-specialist. However, other Heteroptera became favoured material for the investigation of chromosomes and, in 1947, Kullenberg described the process of fertilisation in Miridae. At the same time, quantitative studies appeared on ovariole and testis follicle number in many Heteroptera, although once again studies of the Miridae lagged behind.

Recently attention is being made to the details of the morphology of both reproductives and genitalia throughout Heteroptera consequent to the revival

that has occurred in studies of the higher systematics of the group. In 1954 an attempt was made to elucidate the major groupings in land-bugs, based on structures hitherto ignored or whose significance had been overlooked or misinterpreted (Leston, Pendergrast & Southwood, 1954). Subsequent to this paper comparative studies have been published on the male and female reproductives (Pendergrast, 1957 ; Miyamoto, 1957) ; female genitalia (Scudder, 1959) ; salivary glands (Southwood, 1955) ; eggs (Southwood, 1956) ; sound-production organs and associated behaviour patterns (Leston, 1957 a) ; chromosome numbers and the sex mechanism (Leston, 1957 b, 1958) and wings (Leston, 1960). Studies confined largely to Miridae are discussed below.

It became clear in an investigation of mirid chromosomes that the number of testis follicles in the family varied between species : this was suprising because Kullenberg (1947) had written : " Soweit mit bekannt haben die Capsiden [=Miridae] in jedem der beiden Testikeln sieben Follikeln ". Davis (1955) had found seven ovarioles in four mirid species. Miyamoto (1957, 1959) counted the numbers of ovarioles in many families of Heteroptera, including Miridae. In most of the twenty mirids examined there were seven ovarioles : the only variant, eight, was not distributed along any known systematic line nor does the addition of data on further species (from Carayon, 1950 and Woodward, 1950) suggest other than that *variation from an ovariole number of seven is distributed at haphazard within the family.*

The present study gives counts of testis follicles in as many species as could be collected within a single season, with a view to illuminating systematic and phylogenetic problems within the Miridae. That each result is a numerical one provides an incentive lacking where the presumed systematic character is qualitative and subject to biased evaluation.

MATERIAL AND METHODS

Bugs were collected at localities in Bedfordshire, Hertfordshire, Middlesex, Berkshire and Surrey or, the coastal species, Devon and Cornwall. All dissections were of fresh material, anaesthetised by ethyl chloride and dissected in 0·6 per cent saline. Where the testes were small, convoluted or otherwise obscured they were stained lightly in aceto-orcein, as in routine cytology. Both fifth instar larvae and adult males were used : the pre-mating adult life of many mirids is often surprisingly short (e.g. in *Bryocoris pteridis* (Fall.)) and because of this, or a high incidence of parasitism, a dozen or more species examined gave no results. After mating the testes are shrunken and counting becomes almost impossible.

Biological details of the species examined are given by Southwood & Leston (1959).

THE NUMBERS OF TESTIS FOLLICLES

The results, including re-examination of the species listed by Woodward (1950) and incorporation of two earlier counts, are listed in Table 1.

In the majority of species the number of follicles is constant and symmetrical bilaterally : in some species up to fifty individuals were examined. Two

Table 1—Numbers of testis follicles in Miridae (Hemiptera). (Systematic arrangement and nomenclature after Southwood & Leston, 1959.)

Species	Testis follicle number	Remarks
BRYOCORINAE : Bryocorini		
Monalocoris filicis (L.)	2	
Monaloniini		
Helopeltis antonii Sign.	3	Indonesia : De Jong, 1934
DERAEOCORINAE : Deraeocorini		
Deraeocoris lutescens (Schill.)	2	
D. ruber (L.)	8	
D. olivaceus (F.)	7	
Alloeotomus gothicus (Fall.)	3–4	Variable, see text
PHYILNAE : Phylini		
Lopus decolor (Fall.)	3	
Oncotylus viridiflavus (Goeze)	4–5	Variable, see text
Megalocoleus molliculus (Fall.)	3	
Amblytylus nasutus (Kirschb.)	3	
Macrotylus solitarius (M.-D.)	3	
M. paykulli (Fall.)	3	
Orthonotus rufifrons (Fall.)	3	
Harpocera thoracica (Fall.)	3	
Tytthus pygmaeus (Zett.)	3?	Testes very small
Phylus melanocephalus (L.)	3	One with 2 left, 3 right
P. coryli (L.)	3	
Psallus betuleti (Fall.)	3	
P. ambiguus (Fall.)	3	
P. perrisi Wagner	3	
P. roseus (F.)	3	
P. lepidus Fieber	3	
P. varians (H.-S.)	3	
Atractotomus mali (M.-D.)	3	
A. magnicornis (Fall.)	3	
Plagiognathus albipennis (Fall.)	3	Form off *Artemisia vulgaris*
P. arbustorum (F.)	3	
P. chrysanthemi (Wolff)	3	
Sthenarus roseri (H.-S.)	3	
S. rotermundi (Scholtz)	3	
Asciodema obsoletum (Fieber)	3	
DICYPHINAE : Dicyphini		
Dicyphus constrictus (Bohem.)	1	
D. epilobii Reuter	1	
D. stachydis Reuter	1	
D. annulatus (Wolff)	1	
D. globulifer (Fall.)	1	
ORTHOTYLINAE : Pilophorini		
Pilophorus cinnamopterus (Kirschb.)	2	
Halticini		
Orthocephalus coriaceus (F.)		
Orthotylini	4?	One only examined
Malacocoris chlorizans (Panzer)	2	
Fieberocapsus flaveolus (Reut.)	2	
Cyllecoris histrionicus (L.)	2	
Dryophilocoris flavoquadrimaculatus (De Geer)	2	
Heterocordylus genistae (Scop.)	2	

Table 1—*continued*

Species	Testis follicle number	Remarks
H. tibialis (Hahn)	2	
Heterotoma merioptera (Scop.)	2	
Blepharidopterus angulatus (Fall.)	2	Form *angulatus*
Orthotylus viridinervis (Kirschb.)	2	
O. marginalis Reuter	2	
O. nassatus (F.)	2	One with 3 left, 2 right
O. ochrotrichus Fieber	2	
O. ericetorum	2	
O. adenocarpi (Perris)	2	
O. flavosparsus (Sahlb.)	2	
O. moncreaffi (D. & S.)	2	
Pseudoloxops coccineus (M.-D.)	2	
Cyrtorhinus caricis (Fall.)	1	
Neomecomma bilineatus (Fall.)	2	
Mecomma ambulans (Fall.)	2	
MIRINAE : Mirini		
Lygus maritimus Wagner	7	
L. rugulipennis Poppius	7	
Liocoris tripustulatus (F.)	7	Woodward 1950 ; D. L.
Orthops campestris (L.)	7	
Lygocoris pabulinus (L.)	7	
L. viridis (Fall.)	7	
L. contaminatus (Fall.)	7	
L. lucorum (M.-D.)	7	
Camptozygum pinastri (Fall.)	7	
Plesiocoris rugicollis (Fall.)	7	
Charagochilus gyllenhali (Fall.)	7	
Calocoris quadripunctatus (Vill.)	7	
C. sexguttatus (F.)	7	
C. norvegicus (Gmelin)	7	
C. hispanicus (Gmelin)	7	S. France : Dufour, 1833
Adelphocoris ticinensis (M.-D.)	7	
A. lineolatus (Goeze)	7	
Megacoelum infusum (H.-S.)	7	
Stenotus binotatus (F.)	8	
Miridius quadrivirgatus (Costa)	7	
Phytocoris tiliae (F.)	7	
P. populi (L.)	7	
P. dimidiatus Kirschb.	7	
P. longipennis Flor	7	
P. reuteri Saunders	7	
P. ulmi (L.)	7	
P. varipes Boheman	7	
Capsus ater (L.)	7	Woodward, 1950 ; D. L.
Pantilius tunicatus (F.)	7	
Stenodemini		
Stenodema calcaratum (Fall.)	7	Woodward, 1950 ; D. L.
S. laevigatum (L.)	7	Woodward, 1950 ; D. L.
Notostira elongata (Geoff.)	3	D. L. ; Woodward, 1950 states 7
Megaloceraea recticornis (Geoff.)	7	
Trigonotylus ruficornis (Geoff.)	7	
Leptopterna ferrugata (Fall.)	8	Woodward, 1950 ; D. L.
L. dolabrata (L.)	8	Woodward, 1950 ; D. L.

types of intraspecific variation were noted, individual unilateral variation and indefinite follicle number.

Unilateral variation. Fourteen males, adult or fifth instar, were examined of *Phylus melanocephalus*. Thirteen had three follicles in each testis ; one had two follicles on the left and three on the right. Three *Orthotylus nassatus* were examined : two had two follicles on each side but one had three on the left and two on the right. It is suggested that these odd examples of *P. melanocephalus* and *O. nassatus* represented individual aberrations, the only two in a total of over 1,000 examinations. In the former variation was subtractive, in the latter additive.

Indefinite follicle number. Seven *Alloeotomus gothicus* were examined : the follicles of no two individuals were alike nor was there bilateral symmetry. There may be three short, broad follicles or four short follices of varying breadths, in either case with or without a small supernumerary follicle (Fig. 1).

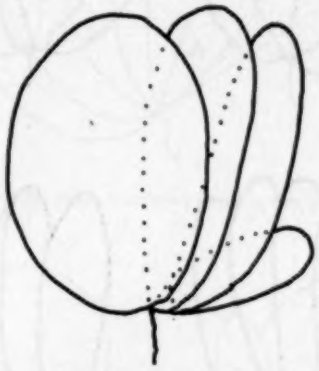

Fig. 1—Testis of *Alloeotomus gothicus*, showing one of the varianta.

It is probable, however, that total volume of each testis is reasonably constant. In general the testis, in being made up of short, loose follicles, resembles that of *Deraeocoris lutescens* rather than the *D. ruber* and *olivaceus* pattern. The supernumerary is always lateral.

Oncotylus viridiflavus has a different type of indefinite follicle number. Eight non-parasitised larvae and adults were examined. There are always four main follicles present, with or without a short lateral supernumerary ; in addition, one of the main, tubular, follicles may be more or less bifid (Fig. 2). There is also a tendency for the follicles to be spiralised, or swollen at base or apex. That which is here regarded as bifurcation may, in fact, be partial fusion of two adjacent follicles is realised—following the latter hypothesis it could be said that the bugs exhibit different stages of reduction from a follicle number of six.

Normal follicle number. With the exceptions noted, follicle number is constant for each species. It is not worth while to give measurements, these varying with the progress of gametogenesis. *Adelphocoris lineolatus*

(Fig. 3) may, in its testis structure, be taken as typical of mirines : each follicle is, in the mature male, at least three times as long as broad. In phylines and orthotylines the ratio of length to width is seldom as great. Deraeocorines, especially *D. ruber* and *D. olivaceus*, approach mirines in this character, dicyphines perhaps phylines. The only bug showing marked variation in follicle width was *Notostira elongata* (Fig. 4).

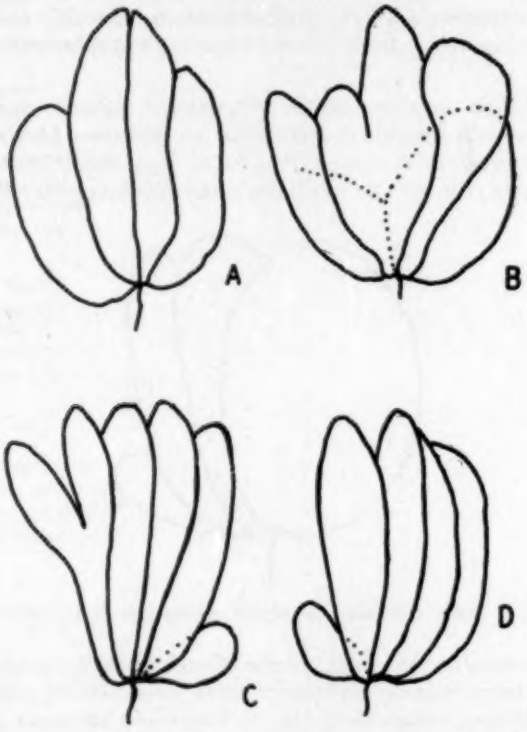

Fig. 2—Testes of *Oncotylus viridiflavus*, showing four of the variants.

Range of follicle numbers. Woodward (1950) and Pendergrast (1956) list the follicle numbers of sixty species of Heteroptera, distributed in twenty-six families (excluding Miridae). The suborder has a range of from one to seven on their data but recently Schrader (1960) reports eight follicles in the pentatomid *Dinocoris rufitarsus* Ruckes. The range in Miridae, based on ninety-four species, is from one to eight, that is, it is as large as the range for the entire suborder of which it is a member. Too few species have been examined in any family other than Miridae for a type number to be postulated.

The generic pattern. Each genus, with one exception, has a constant follicle number, one which is imposed, in general, at subfamily level. In *Deraeocoris* this is not the case : however, until recently *D. lutescens* was

placed in *Camptobrochis*. It would seem as if the evidence upon which Knight (1921) constructed his interpretation of *Deraeocoris*, in which he was followed by Carvalho & Leston (1952), requires re-assessment : certainly both in life history and general appearance *D. lutescens* differs considerably from the remaining British members of the genus. Kelton (1959) also suggests the genus may be polyphyletic.

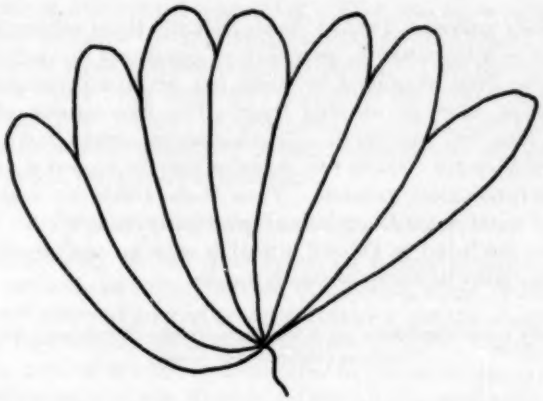

Fig. 3—Testis of *Adelphocoris lineolatus*, showing the typical mirine form.

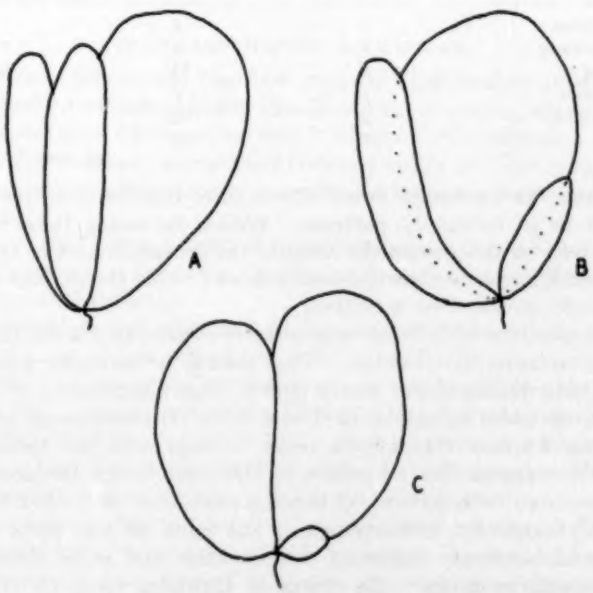

Fig. 4—Testes of *Notostira elongata*, showing three of the variants.

Two genera, *Stenotus* and *Leptopterna*, have eight follicles whereas subfamily pattern suggests that they should have seven. From the data of Carayon (1950) and Miyamoto (1957) it appears that eight ovarioles occur in certain genera of Reduviidae and Miridae, families in which most genera have seven : it may be that in both ovariole and follicle numbers eight can appear not infrequently in groups having a type number of seven. This is also apparently the case as between *Deraeocoris ruber* and *D. olivaceus*.

The subfamily pattern. Table 1 shows that the three subfamilies examined in most detail exhibit what is probably a significant modality (that other subfamilies have been examined in much less detail has decided the author against statistical analysis at this stage). The five species of Dicyphinae inspected fall into two subgenera, *Dicyphus* sensu stricto and (*globulifer* and *annulatus*) *Brachyceraea* : these two perhaps may be regarded as good genera on general morphological grounds. Thus there seems no reason to doubt, that the modal number for Dicyphinae is also fairly well defined. The derived modal numbers are listed in Table 2, together with an analysis of the numbers of species conforming to each subfamily mode.

Table 2—Subfamily modal numbers of testis follicles in Miridae (Hemiptera), showing numbers of species conforming to modes.

Subfamily	Modal number	Number of species examined	Number of species conforming to mode
Bryocorinae	?	2	?
Deraeocorinae	?	4	?
Phylinae	3	25	24
Dicyphinae	1	5	5
Orthotylinae	2	22	20
Mirinae	7	36	32

Apart from the anomalies noted above there remain three species which fail to conform to subfamily patterns. Before discussing these it must be pointed out that for the present the limits of the subfamilies are to be construed as those generally accepted (see discussion below) : that the present subfamilies may be wrongly constructed is realised.

Only one specimen of *Orthocephalus coriaceus* was available for examination. It appeared to have four follicles. This species is currently placed in the orthotyline tribe Halticini but Slater (1950), after examination of the female genitalia, wrote under its synonym *O. mutabilis* "It seems most questionable to the author whether this species really belongs with the Orthotylinae". Kelton (1959) suggests that all genera of Halticini except the nominotypical are some way from Orthotylinae, at least on characters presented by the male genitalia. Cytologically, Orthotylinae is the most diverse mirid subfamily. The tribal and subfamily status of *Orthocephalus* and other Halticini must, therefore, remain in doubt : the status of Halticini vis à vis Orthotylinae requires examining anew.

The systematic position of *Cyrtorhinus caricis* is discussed at length by Carvalho & Southwood (1955), who saw no reason for distinguishing it other than as a genus of Orthotylini. However, the single-follicle testis is remarkably small even when staining shows that it is full of ripe sperm and therefore at maximum distension. The eight males examined exhibited no obvious variation in follicle number or shape.

Forty-five non-parasitized individuals were examined of *Notostira elongata*, all of them of the second annual generation. Each had three follicles but with much individual variation in the relative sizes of the follicle (Fig. 4). In general, two were of equal size whilst a third varied. That this bug is a typical Stenodemini has never been disputed ; although much has been written on its life cycle and colour forms. It is concluded that in this instance follicle number has deviated from subfamily pattern considerably though it remains, on all other grounds, a typical Stenodemini.

FOLLICLE NUMBER AND THE FAMILY

No one number may be taken as typifying follicle number in a family. However, the presence of seven follicles in Mirinae, some Deraeocorinae, in such a generalised cimicoid-mirioid group as Nabidae and elsewhere sporadically throughout the Heteroptera (data from Woodward, 1950 ; Carayon, 1950) can only be taken to mean this is the basic number in the entire group and probably the ancestral type number for Miridae. Thus all the subfamily types below seven, it is postulated, have been derived by reduction. The additive process is perhaps confined to the few instances where eight follicles appear in groups normally with seven.

THE CLASSIFICATION OF MIRIDAE

Knight (1923) formulated the first modern classification of Miridae ; in 1941 he restated his scheme of higher classification, recognising nine subfamilies. Of these, the status of Clivineminae and " Mirinae " (Stenodemini), have been reduced. Knight's scheme as modified is shown in Fig. 5. The various studies which have suggested alterations to or confirmed the arrangement of Fig. 5 are reviewed below.

Kullenberg (1947), from a study of female genitalia, suggested a relationship between *Bothynotus* and *Dicyphus*, that is, between members of Deraeocorinae (Clivinemini) and Dicyphinae.

Slater (1950) suggested relationships based upon the structure of the bursa copulatrix and associated structures. He regarded Bryocorinae as being primitive, with Phylinae and Dicyphinae also presenting a generalised type of female genitalia ; postulated a link between Phylinae and Orthotylinae ; showed that Hyaliodini (a non-British tribe now placed in the Deraeocorinae) perhaps linked Deraeocorinae with Dicyphinae ; confirmed the placement of Clivinemini within Deraeocorinae and suggested the latter as ancestral to Mirinae. On Slater's observations it is possible to construct a family tree only if Orthotylinae is regarded as polyphyletic : he found that certain Halticini female genitalia suggested a link with Deraeocorinae whilst *Semium*—currently placed in Orthotylinae—would relate the subfamily to a Phylinae-

Dicyphinae stem. Davis (1955), working with four species, clarifies the structure of the female reproductives.

Wagner (1955), basing his studies principally on male genitalia, groups the subfamilies into three : Phylinae, Orthotylinae, the remainder. His inter-relationship diagram is unacceptable in that the simple hair-like arolia of Deraeocorinae and Dicyphinae would be re-acquisitions of a primitive character, a mode of thought incompatible with Dollo's principle.

Carvalho (1956) introducted Palaucorinae, a new and monotypic subfamily. From the description and figures it could well be a somewhat isolated deraeocorine.

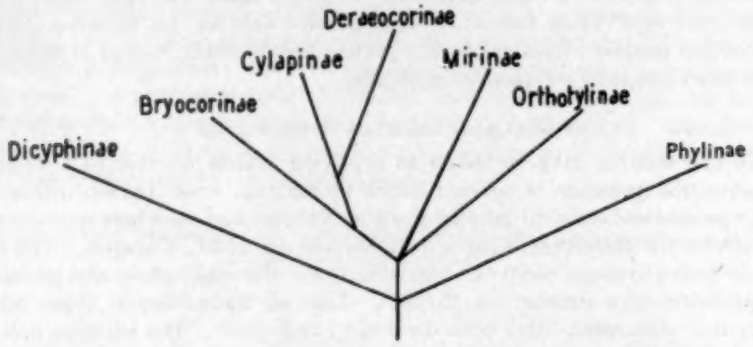

Fig. 5—The inter-relationship of the subfamilies of Miridae according to Knight (1941) as modified by later authors.

The chromosome numbers of some seventy mirids have been given (Leston, 1957 b and further data in Southwood & Leston, 1959). Although in Orthotylinae only the nominotypical tribe has been examined the data suggest that this is a most variable subfamily. Deraeocorinae, Bryocorinae, Phylinae and Mirinae retain, for the most part, the same diploid number : $2n=32A+X+Y$. There is some minor reduction in the number of autosomes in many species (due principally to loss of the microchromosomes). It is assumed that $32A+X+Y$ is the ancestral number in the family. Dicyphinae have undergone fragmentation of many chromosomes and the three species known cytologically have $2n=46A+X+Y$: this could have arisen by polyploidy from a hypothetical $23A+X+Y$, a type within the range of Orthotylinae—the chromosomes of *Dicyphus* are remarkably small.

The eggs of Miridae were studied by Kullenberg (1942, 1943) and Southwood (1956) : the latter concluded " The eggs do not appear to exhibit any subfamily characteristics in the Miridae, but it is very probable that some would be found if the number and distribution of the pseudomicropyles were further investigated. However, the eggs of closely related genera are similar.... " It is noteworthy that the two mirids having exophytic oviposition, and eggs modified in accordance, are two orthotylines, *Malacocoris* and *Strongylocoris*, that are but remotely related—in this as in most other characteristics Orthotylinae are less homogeneous than the other subfamilies.

Carayon (1958) has attached the family Isometopidae to Miridae, treating the former as a subfamily. He gives little detailed information on eggs, reproductives or genitalia nor does he suggest a relationship to any one of the existing mirid subfamilies. If he is correct in his interpretation then Isometopinae must be regarded as an early offshoot of Mirinae, for it has retained ocelli. However, the presence of but one membrane cell in Bryocorinae and Isometopinae may be a case of analogy rather than homology : only a tracheal study can settle this. Scudder (1959) points out that the female genitalia of Isometopidae are close to those of Miridae. Recent workers, e.g. China & Miller (1959), have overlooked Diphlebinae, an isometopid subfamily (Bergroth, 1925).

Hesse (1947), in a paper that has been overlooked by later workers, briefly describes the eggs of an isometopid. Such positive features as he notes, but more especially the flattened and oblique operculum, indicate that the eggs are of mirid type.

Kelton (1959) surveys the male genitalia of nearly 150 species, principally nearctic. He reaches many conclusions as to systematic relationships. The Bryocorinae are isolated and exhibit two patterns of aedeagus. The Deraeocorinae also appear to be distinctive, with a suggestion that Mirinae may have evolved therefrom. Cylapinae show a possible relationship only in the vesica, which in *Cylapus* is similar to that of some Halticini and in *Fulvius* to the Dicyphinae. Phylinae have a simple vesica and show a possible relationship only to Pilophorini : this latter, a tribe of Orthotylinae, is on aedeagal characters polyphyletic. Dicyphinae are apparently closer to Cylapinae than to any other group.

On the whole the aedeagus of Orthotylinae suggests this too is an isolated group, though highly specialised. Halticini and Orthotylini have certain features in common but many genera currently placed in one or the other of these tribes suggest a relationship to neither. *Semium* and *Pilophorus* show little connection with Orthotylinae, though both are placed therein on general characters, in the form of male or female genitalia.

Mirinae have a specialised aedeagus unrelated to that of other groups except Deraeocorinae. In contradistinction to Orthotylinae the group is homogeneous.

There remain for evaluation the traditional features used in diagnosing the subfamilies. These features—pronotal collar, wing cells, the pretarsus—have been proved to work satisfactorily (Knight, 1941 ; Carvalho, 1952, 1955 ; Carvalho & Leston, 1952 ; etc.). Almost all of the many thousands of known mirids can be placed quite readily in existing groups and, as the present study shows on follicle number, Dicyphinae, Orthotylinae, Phylinae and Mirinae are well defined entities as, on other grounds is Bryocorinae. However, whereas these features enable groups to be diagnosed they do not enable groups to be placed in an evolutionary sequence.

On a pretarsal character two subfamilies, Mirinae and Orthotylinae have always been closely associated. But acceptance of this similarity (both possess membranous arolia) as evidence of monophyleticity is contradicted by consideration of almost every other character, both old and new. It is therefore

concluded that this is an example of convergence. Freeing Mirinae from association with Orthotylinae enables it to be associated with Deraeocorinae ; on pretarsal characters Deraeocorinae and Mirinae are dissimilar but on most other characters—not least the possession of a pronotal collar—they have much in common. The relationship between Phylinae and Orthotylinae barred on pretarsal structure is, on almost all other evidence, so close that a few genera cannot be placed with certitude in either, at least on genitalic features : but the evidence gathered together above on Orthotylinae also leads to the belief that perhaps a further subfamily requires erection here or, at least, that a revision of the Orthotylinae-Phylinae block at tribal level might clarify the position.

The status of Dicyphinae as a subfamily, denied by Carvalho (1952, 1955, 1957–60), is amply supported by the evidence of chromosome number, follicle number and other features : that it has features in common with Orthotylinae-Phylinae is also suggested, mainly on the structure of the genitalia and on the reduced follicle number. Unfortunately little can be said on Cylapinae : its pretarsal characters are close to those of Deraeocorinae but once these are discounted there remains only Kelton's evidence. Because the group is overwhelmingly tropical it has scarcely, as yet, been investigated—follicle number and chromosome number are both unknown. However, a pronotal collar is often present, apparently of the Deraeocorinae-Mirinae type, though subject to much modification in many genera. These features—collar, pretarsus, forewings—are figured in detail by Carvalho (1955).

Non-morphological evidence must be mentioned. Although of probable early Tertiary origin—the bulk of bug families arose in the Mesozoic—all the subfamilies are of world-wide distribution : such limitation as occurs, for example the scarcity of cylapines and bryocorines in the north temperate zone, must be looked upon as climatic in origin rather than as a reflection of areas of autochthony. It has been shown by statistical analyses of tropical island faunas (Leston, 1957 c) and by correlation of trap captures with local populations (Southwood, 1960) that mirids are able to migrate for considerable distances. Probably the plastic feeding habits of many groups also enable them to exploit new localities. It is concluded that present geographical distribution, at least at subfamily level, throws no light on the major evolutionary problem.

Finally, feeding habits. Although, as mentioned, many mirids are exceedingly plastic in food choice, certain groups are of restricted diet. Table 3 lists a number of pest genera, compiled from Evans (1952), Knight (1941), Costa Lima (1940) and Southwood & Leston (1959) : whilst not comprehensive it is probable that few genera of importance have been overlooked. From this it is seen that the great majority of pest species are, Bryocorinae (with some Mirinae) in the tropics, and, in temperate zones, almost entirely Mirinae. There are no pests in Deraeocorinae or Cylapinae. Now the distribution of pest genera within the subfamilies can only be a reflection of the feeding habit—and sizes—of the groups. From the data given on 200 British mirids by Southwood & Leston (1959) the feeding habits of the subfamilies found in Britain can also be deduced ; some similar evidence can be obtained by

evaluating the details on North American species given briefly by Blatchley (1926) and Knight (1941).

Table 3—List of genera of Miridae containing pest species, to indicate distribution of phytophagy in the subfamilies (nomenclature after Carvalho, 1957–60).

Bryocoropsis	BRYOCORINAE	*Lygus*	MIRINAE
Calocoris	MIRINAE	*Macrolophus*	DICYPHINAE
Campylomma	PHYLINAE	*Megacoelum*	MIRINAE
Collaria	MIRINAE	*Monalonion*	BRYOCORINAE
Cyrtopeltis	DICYPHINAE	*Neurocolpus*	MIRINAE
Distantiella	BRYOCORINAE	*Orthops*	MIRINAE
Helopeltis	BRYOCORINAE	*Pachypeltis* (= *Disphinctus*)	BRYOCORINAE
Horcias	MIRINAE		
Hyalopeplus	MIRINAE	*Parachamus*	BRYOCORINAE
Leptopterna	MIRINAE	*Plesiocoris*	MIRINAE
Lycidocoris	BRYOCORINAE	*Psallus*	PHYLINAE
Lygidea	MIRINAE	*Sahlbergella*	BRYOCORINAE
Lygidolon	MIRINAE	*Taylorilygus*	MIRINAE
Lygocoris	MIRINAE	*Tenthecoris*	BRYOCORINAE

From an analysis it appears that Deraeocorinae and Cylapinae are exclusively predatory. Mirinae are mainly phytophagous, with a few carnivorous genera. Bryocorinae are exclusively phytophagous. Most Phylinae are mixed feeders. Dicyphinae contains both predatory and phytophagous species : it is largely specialised for a life upon plants with glandular or upright hairs. Orthotylinae contains both mixed feeders and exclusively carnivorous forms. Isometopidae are exclusively predatory.

It is clear that feeding habits cut across the intersubfamily relationships already postulated although the " reduced follicle number " group approximates to the " mixed feeding " group ; nor can feeding habits be associated with tarsal or pretarsal structure.

THE STATUS OF MIRIDAE

Currently Miridae is regarded as a family of Cimicoidea, with Isometopidae closely allied, but unfortunately Cimicoidea has not been re-defined since 1912 (Reuter) ; however, the literature on the group is extensive and mostly concerned with the placing of aberrent genera in the families Miridae, Isometopidae, Anthocoridae or Nabidae (McAtee & Malloch, 1924 ; Bergroth, 1925 ; China & Myers, 1929 ; Carayon, 1958, etc.). The families generally regarded as comprising Cimicoidae are : Nabidae (including Velocipedidae), Polyctenidae, Joppeicidae (excluded by China & Miller, 1959, but included by all other students of the group) Cimicidae (including Anthocoridae), Microphysidae, Miridae and Isometopidae. The attaching of Isometopidae to Miridae by Carayon (1958) is justified by a considerable number of characters; some have been already discussed and others are listed below : however, a case could be made out for retaining Isometopidae as a family, raising Bryocorinae to family status and placing both, with a restricted Miridae, in a revived superfamily Mirioidea. This would still leave a heterogeneous Cimicoidea for on many characters, not least the eggs, the Nabidae, including Velocipedinae, are some

way removed from Cimicidae and Microphysidae. On egg characters, euphorine parasitism and, it is now suggested, on forewing venation, it is probable that Miridae sensu lat. originated from a cimicoid close to Nabidae : therefore, in view of the lack of knowledge of nabid structure and biology (with the exception of Nabinae), and the apparent lack of annectant forms between Nabidae and Cimicidae, or at least clues to these, it seems best to retain a blanket Cimicoidea for the time being. Should Mirioidea be accepted it can be separated from Cimicoidea sensu stricto on the characters given in the diagnosis below.

The relationships here suggested are shown in Fig. 6. To the information given in the figure should be added the fact that the mirid transmembranal venation is primarily one of two cells, biareolate. This condition has distal R and M fused as the dividing vein between the anterior cell, sc, and the posterior cell, r+m. The posterior vein of cell r+m is Cu+1V (Leston, 1960). This condition can be derived from the nabinae-velocepedinae venation by an anterior shift of distal M and a similar shift of distal 1V. As Bergroth (1925) pointed out, though later workers have overlooked the fact, some isometopines and bryocorines retain traces of the biareolate condition. These is also on the forewing of many Miridae, especially Mirinae, a false vein (Leston, 1960), the anal vein of Knight (1941) : this structure is also present in *Scotomedes* (Nabidae : Velocepidinae) and may perhaps be homologous in the two groups. Euphorine parasites, well known to occur in Miridae, have been found too in Nabidae (Leston, unpubl.)

It follows from this that although Isometopinae are shown in Fig. 6, as an early offshoot of the main mirid stem they have lost a number of features retained by the higher Miridae : it is probable that the early mirids were far larger than the present day minute isometopines, but the presence of ocelli is to be looked upon as retention of a primitive feature. There is an additional group in the old Isometopidae, Bergroth's subfamily Diphlebinae : this must now be regarded as a tribe.

The evidence given above, stemming largely from the investigations of Slater (1950) and Kelton (1959) of female and male genitalia, shows that the subfamilies Phylinae and Orthtyolinae are scarcely distinct : however, the bulk of the genera fall within one or other of the groups. The relationship could best be expressed by the erection of further tribes, some of which must originate from or perhaps below the phyline-orthotyline split : whether these groups—*Semium*, *Orthocephalus*, etc.—be attached to one or other of the subfamilies or further subfamilies be erected is a matter of personal preference until further evidence accrues. The genitalic features which suggest links between some genera of deraeocorines with dicyphines, deraecorines with orthotylines and dicyphines with cylapines may all be the result of retention of the generalised structure of the higher mirids.

DEFINITION AND LIMITS OF MIRIDAE

Many of the diagnostic features have already been discussed by Carayon (1958) and Kullenberg (1947) but not in the form of a definition. The group is diagnosed :

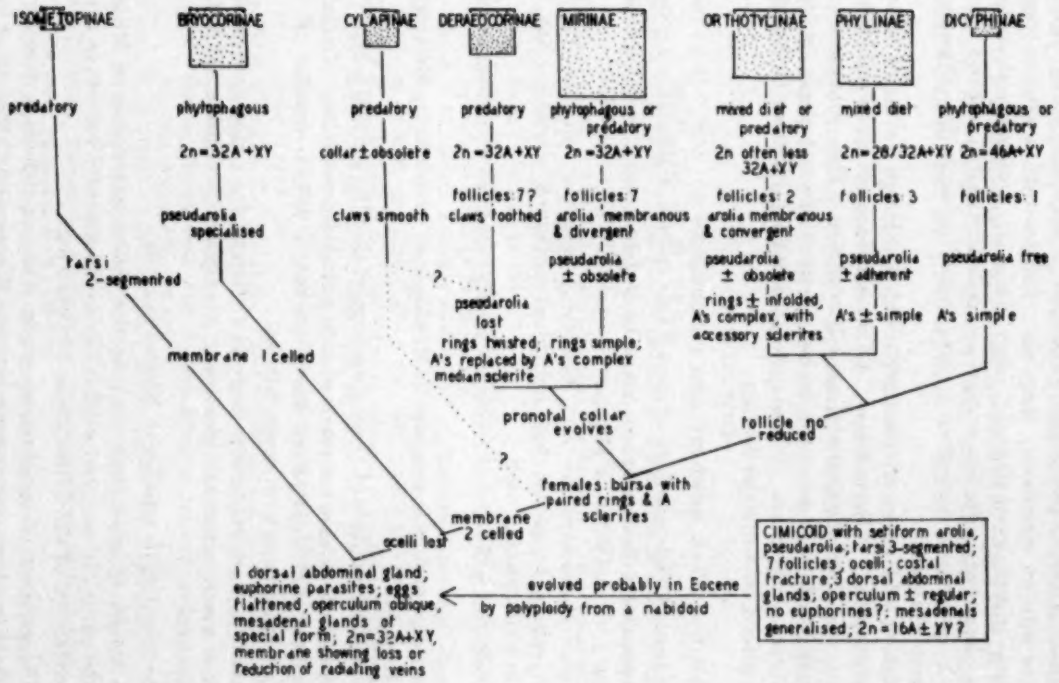

Fig. 6—The inter-relationship of the subfamilies of Miridae arrived at by the present study. For further information see text. The subfamily rectangles are proportionate in area to the number of species in each.

Heteroptera Cimicomorpha, near Nabidae ; forewings with a costal fracture, anterior furrow remote from the costal margin (" wide embolium "), with two closed membranes cells—sc and r+m— or these further reduced ; a single dorsal abdominal gland ; males with paired, elongate, tubular mesadenal glands, without flabellate processes ; mesadenal glands opening along with the sperm ducts into an ejaculatory ampoule ; females with a median vaginal diverticulum (pseudospermatheca) ; eggs with an asymmetrical, oblique, operculum, deposited, with few exceptions, endophytically ; diploid number 32A+X+Y or derived therefrom ; parasitized by euphorine Braconidae ; ocelli present or absent.

The existing subfamilies are retained in Fig. 6 although the major divisions are : 1. Isometopinae ; 2. Bryocorinae ; 3. Deraeocorinae+Mirinae and probably Cylapinae ; 4. Phylinae/Orthotylinae+Dicyphinae. The subfamilies are retained until such time as 1. the higher groups of Isometopinae, including Diphlebini, are worked out ; 2. the systematics of the Phylinae-Orthotylinae group are placed on a sounder footing.

SUMMARY AND CONCLUSIONS

1. The testis follicle numbers of ninety-four species of Miridae are given.

2. Subfamilies exhibit marked modality in follicle number : Phylinae 3, Dicyphinae 1, Orthotylinae 2, Mirinae 7.

3. *Phylus melanocephalus* and *Orthotylus nassatus* conform to their respective subfamily modes but individual unilateral variation has been detected in a singleton of each.

4. *Alloeotomus gothicus* and *Oncotylus viridiflavus* have an indefinite follicle number.

5. The range of follicle numbers in Miridae is as in the entire Heteroptera, viz., one to eight.

6. The follicle numbers of *Deraeocoris* suggest that the genus is polyphyletic.

7. Type numbers have been arrived at in general by reduction. *Deraeocoris ruber*, *Stenotus* and *Leptopterna* have evolved a follicle number of eight additively from groups with seven follicles.

8. Variation from subfamily mode in *Orthocephalus coriaceus* is probably indicative of wrong systematic placement ; in *Cyrtorhinus caricis* and *Notostira* of specialisation.

9. The type follicle number of Miridae is seven.

10. A review of work since 1941 on the higher systematics of Miridae is given ; the currently accepted subfamilies are zoologically valid taxa with the possible exception of the Orthotylinae-Phylinae pair.

11. The presence of membranous arolia does not delimit a monophyletic block : there has been convergence between Mirinae and Orthotylinae in this.

12. Isometopinae, Deraeocorinae and Cylapinae are predatory ; Bryocorinae phytophagous ; Mirinae largely phytophagous, with some predatory genera ; Phylinae generally mixed feeders ; Dicyphinae contains predatory and phytophagous species ; Orthotylinae mixed feeders and predators.

13. Miridae perhaps arose from a nabid-like ancestor ; it is re-defined. The main constituents are : a. Isometopinae ; b. Bryocorinae ; c. Mirinae +Deraeocorinae+(?) Cylapinae ; d. Dicyphinae+Orthotylinae/Phylinae.

14. Isometopinae are primitive in having retained ocelli but the two-celled forewing membrane, derived from the nabid pattern, is more primitive than the one-celled.

15. The genitalic similarities noted between some species of Deraeocorinae, Cylapinae, Dicyphinae, and Orthotylinae are interpreted as retentions of generalised features of the group (c)+(d).

ACKNOWLEDGMENTS

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THE ECOLOGICAL DISTRIBUTION OF SMALL MAMMALS IN NORTH-WEST SCOTLAND

BY

M. J. DELANY

Department of Zoology, University of Southampton

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(With 1 figure in the text)

During the summers of 1957 to 1960 a variety of habitats, including woodland, moorland and agricultural land, have been trapped for small mammals at Applecross, Wester Ross. Traps were also set at two other localities on the mainland. The catches included *Sorex araneus*, *S. minutus*, *Neomys fodiens*, *Apodemus sylvaticus*, *Clethrionomys glareolus* and *Microtus agrestis*. As many habitats as possible have been examined on the Islands of South Rona, Raasay, Rhum, Mull, Colonsay, Lewis, North and South Uist and Barra although there was usually less variety in the vegetation on the islands. On the islands, except Mull, less species are present than on the mainland.

At Applecross, *Apodemus* was common and ubiquitous being most numerous in deciduous wood and farm land. *Clethrionomys* was less widespread and most numerous in woodland. On the Island of Mull the ecological situation appeared similar to the mainland but on the remaining islands *Apodemus* was apparently less frequent. *Clethrionomys* was common on Raasay and Mull. *Microtus* was widespread and trapped in small numbers. It was least common in deciduous woodland. *Mus* occurred in fields in the Outer Hebrides and the Island of Colonsay. *S. minutus* was particularly infrequent and no more abundant on islands from which *S. araneus* was absent.

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INTRODUCTION

The Inner and Outer Hebrides, in north-west Scotland, support a small mammal fauna which varies from island to island. On the adjacent mainland the long-tailed field mouse (*Apodemus sylvaticus* (L.)), bank vole (*Clethrionomys glareolus* Schreb.), field vole (*Microtus agrestis* (L.)), common shrew (*Sorex araneus* L.), pygmy shrew (*S. minutus* L.) and water shrew (*Neomys fodiens* Schreb.) are all present whilst on most islands one or more of these species is absent. Between 1957 and 1960 small mammals were trapped at three localities on the mainland, five islands in the Inner Hebrides and four in the Outer Hebrides. The purposes of the present paper are to determine the types of habitat occupied by the various species on the mainland and to see if they are the same on the islands where the number of species is frequently depleted.

Previous work on small mammals in this area has largely consisted of a series of taxonomic papers by de Winton (1895), Barrett-Hamilton (1899), Miller (1908), Barrett-Hamilton & Hinton (1913 a, 1913 b), Hinton (1914), Montagu (1922), Warwick (1940), Steven (1953) and Delany & Bishop (1960). Additional information on distribution has been provided by Millais (1904–06), Barrett-Hamilton & Hinton (1910–21), Bertram (1939) and Warwick (1939). Few ecological studies have been attempted. They have included the work of Harrisson & Moy-Thomas (1933) and Boyd (1959) on the mice of St. Kilda, Elton (1938) and Warwick (1938) on the small mammals of the Islands of Pabbay and Barra respectively and Delany (1957) on the small mammals of a Dumbartonshire oakwood. No earlier work has been as extensive as the present survey.

A total of 1158 small mammals have been caught in just over 8,500 trap nights although reference has not been made to all these results. On the mainland, Applecross was visited in August 1957–60, September, 1957 and late July, 1960 ; Laga, Ardnamurchan in September, 1958 and August, 1959 ; and Taynuilt, Argyllshire in April/May, 1958. In the Inner Hebrides the Island of Mull was visited in May and September, 1958 and July, 1959 ; and the Islands of South Rona, Raasay, Rhum and Colonsay in July/August 1958, August 1957, July 1959 and August 1959, respectively. Of the Outer Hebrides trappings were made on the Island of Lewis in August 1958 and September, 1960 ; the Island of North Uist in August/September, 1960 ; the Island of South Uist in July, 1959 and August/September, 1960 ; and the Island of Barra in July, 1959 and August, 1960. The situation of each locality is shown in Fig. 1.

Topographically, north-west Scotland is a mountainous region possessing a much indented coastline and having an abundance of islands, both large and small, at distances of up to a hundred miles from the mainland. The vegetation consists of considerable expanses of grass and heather moor with patches of woodland and agricultural land, particularly in more sheltered situations. Few natural woodlands remain and it is probable that of those examined only the oak-birch wood on the east coast of Colonsay falls within this category. The mixed woods, which are predominantly deciduous, have generally been planted on private estates. They contain a relatively large number of tree species. Many of the coniferous woods e.g. Fearnoch Forest, Salen Forest,

Fig. 1—Map showing fifteen localities at which small mammals were trapped, 1957-60. 1, 2, 3, Island of Lewis ; 4, Island of North Uist ; 5, 6, Island of South Uist ; 7, Island of Barra ; 8, Island of South Rona ; 9, Island of Raasay ; 10, Island of Rhum ; 11, Island of Mull ; 12, Island of Colonsay and 13, 14, 15, mainland.

Raasay Forest and Balallan Plantation, have been planted by the Forestry Commission. On the Outer Hebrides a situation was trapped which has no apparent equivalent on the mainland or the Inner Hebrides. This was the low-lying machair, or calcareous natural grassland which is found on the west coasts between the sand dunes and the peat. As wide a range of vegetation types as possible were examined in each locality although it was found that the islands generally contained less diversity. As woodland and agricultural land were usually situated in sheltered valleys most trapping was undertaken on comparatively low ground. Two types of habitat were not examined in detail as it was assumed, and confirmed by limited trapping, that they supported an extremely low mammal population. They were, patches of mature, dense coniferous wood where the floor consisted of dead, fallen needles and expanses of short *Calluna* and associated species growing on peat which offered little cover and an impenetrable substrate.

The geographical distribution of the species caught during the survey is given in Table 1 and the number caught in each of four main habitat types (deciduous woodland, coniferous woodland, agricultural land and moorland) are given in Tables 2 to 5.

Table 1—Geographical distribution of small mammals caught during the survey, 1957–60.

	S. araneus	*S. minutus*	*Neomys*	*Microtus*	*Clethrionomys*	*Apodemus*	*Mus*
Mainland	X	X	X	X	X	X	—
Island of S. Rona	X	X	—	—	—	X	—
Island of Raasay	X	X	X	—	X	X	—
Island of Rhum	—	X	—	—	—	X	—
Island of Mull	X	X	X	X	X	X	—
Island of Colonsay	—	X	—	—	—	X	X
Island of Lewis	—	X	—	—	—	X	X
Island of N. Uist	—	X	—	X	—	X	X
Island of S. Uist	—	X	—	X	—	X	X
Island of Barra	—	X	—	—	—	X	X

X—trapped during the survey.

TRAPPING METHODS

Longworth traps (Chitty & Kempson, 1949) were used throughout the survey and were invariably baited with a few grains of oatmeal. They were set in lines with a five yard (pace) interval between each trap and were examined daily when their catch was removed. In the following accounts of the mainland and Inner Island trappings, the number of traps set, or the number of trap nights, is calculated on the basis of each trap having been in a line of traps and having been set for three nights. Thus, reference to thirty trap nights implies that a line of ten traps has been set in that habitat for three consecutive nights. In the Outer Isles traps were set in the same place for only one night. Caution must be exercised in comparing the numbers of one species against another as some species (notably *Microtus*) may be more reluctant to enter traps.

DISTRIBUTION OF SMALL MAMMALS

With the exception of the house mouse (*Mus musculus* L.) which also occurs on the mainland, Raasay, Mull and Rhum, the species listed in Table 1 probably

Table 2—Catches of small mammals in deciduous or predominantly deciduous woodland and associated scrub in various localities in north-west Scotland, 1957–60.

Locality	Date	Trap nights	*S. araneus*	*S. minutus*	*Neomys*	*Microtus*	*Clethrionomys*	*Apodemus*
Applecross	1957	102	2	—	2	—	16	32
"	1958	96	2	—	—	—	10	18
"	1959	75	—	—	—	—	5	7
"	1960	75	—	—	—	1	4	13
Laga	1958	102	3	—	—	—	7	12
"	1959	150	—	—	—	2	10	22
Fearnoch Forest	1958	285	19	5	—	—	2	2
Island of Mull	v. 1958	210	1	1	2	3	17	15
"	ix. 1958	180	3	—	—	—	29	10
"	vii. 1959	150	2	—	—	—	13	21
Island of South Rona	1958	144	2	1	—	—	—	—
Island of Rhum	1959	99	—	3	—	—	—	5
Island of Colonsay	1959	225	—	—	—	—	—	14
Island of Lewis	1958	99	—	1	—	—	—	8
"	1960	22	—	—	—	—	—	—
Island of Barra	1959	48	—	—	—	—	—	3
"	1960	10	—	—	—	—	—	—

Traps in the Outer Hebrides were moved after one night and the remainder after three nights.

Table 3—Catches of small mammals in coniferous woodland and associated scrub in various localities in north-west Scotland, 1957–60.

Locality	Date	Trap nights	*S. araneus*	*S. minutus*	*Neomys*	*Microtus*	*Clethrionomys*	*Apodemus*
Applecross	1957	45	—	—	—	—	4	8
"	1958	75	1	—	—	4	12	3
"	1959	60	—	—	—	1	3	2
"	1960	60	—	—	—	—	11	6
Fearnoch Forest	1958	210	17	—	—	1	4	—
Island of Mull	v. 1958	21	1	—	—	1	2	—
"	ix. 1958	15	—	—	—	3	2	—
"	vii. 1959	30	1	—	—	1	6	1
Island of Raasay	1957	255	21	1	3	—	51	16
Island of Lewis	1958	25	—	—	—	—	—	—

Traps in the Outer Hebrides were moved after one night and the remainder after three nights.

Table 4—Catches of small mammals in agricultural land, including machair, in various localities in north-west Scotland, 1957–60.

Locality	Date	Trap nights	*S. araneus*	*S. minutus*	*Neomys*	*Microtus*	*Clethrionomys*	*Apodemus*	*Mus*
Applecross	1957	30	—	—	—	1	2	7	—
"	1958	87	1	—	1	—	—	11	—
"	1959	75	—	—	—	—	—	23	—
"	1960	75	1	—	—	—	—	17	—
Lagg	1958	30	—	—	—	—	—	—	—
Island of Mull	v. 1958	15	2	—	—	—	1	—	—
"	ix. 1958	15	4	—	—	—	—	5	—
"	vii. 1959	45	—	—	—	2	1	5	—
Island of Raasay	1957	117	10	—	—	—	13	6	—
Island of Rhum	1959	21	—	—	—	—	—	2	—
Island of Colonsay	1959	150	—	1	—	—	—	8	16
Island of Lewis	1958	75	—	—	—	—	—	1	—
"	1960	206	—	—	—	—	—	14	11
Island of North Uist	1960	290	—	1	—	7	—	15	17
Island of South Uist	1960	401	—	—	—	2	—	13	14
Island of Barra	1959	53	—	—	—	—	—	—	3
"	1960	162	—	—	—	—	—	12	1

Traps in the Outer Hebrides were moved after one night and the remainder after three nights.

Table 5—Catches of small mammals in *Molinia*, *Calluna* and *Festuca* moorland, in various localities in north-west Scotland, 1957–60.

Locality	Date	Trap nights	*S. araneus*	*S. minutus*	*Neomys*	*Microtus*	*Clethrionomys*	*Apodemus*	*Mus*
Applecross	1957	90	5	—	—	2	—	7	—
"	1958	120	4	—	—	1	2	5	—
"	1959	90	1	—	—	—	—	10	—
"	1960	90	3	—	—	—	—	5	—
Fearnoch Forest	1958	30	1	—	—	—	—	—	—
Island of Mull	v. 1958	135	11	—	—	3	1	2	—
"	ix. 1958	60	3	—	—	4	—	—	—
"	vii. 1959	60	3	—	1	3	—	3	—
Island of South Rona	1958	144	1	1	—	—	—	4	—
Island of Rhum	1959	15	—	—	—	—	—	—	—
Island of Colonsay	1959	75	—	—	—	—	—	3	—
Island of North Uist	1960	35	—	1	—	1	—	—	1
Island of South Uist	1959	110	—	—	—	—	—	4	—
"	1960	77	—	—	—	1	—	—	—

Traps in the Outer Hebrides were moved after one night and the remainder after three nights. Sixty-nine of the traps on South Uist were not set in trap lines.

include all those present. Several of the records have not been published previously. They are *Neomys* on Mull and Raasay and both species of *Sorex* as well as *Apodemus* on Raasay. The first records of mammals were obtained from South Rona during the survey although a preliminary note has already been published (Delany & Copland, 1960).

Several island species and subspecies, particularly of *Apodemus*, have been described. As many are of dubious validity (Matthews, 1952 ; Delany, 1959) and as their inclusion here would serve only to complicate nomenclature it has been decided to omit subspecific names and to refer to field mice as *A. sylvaticus* and the voles as *C. glareolus* and *M. agrestis*.

MAINLAND TRAPPINGS

Applecross

In the vicinity of Applecross large areas consist of grass and heather moor populated by sheep and deer. Some of the lower ground makes good agricultural land and there is also a small amount of planted woodland. The area is mountainous and elevations are reached locally of over 2,000ft. Traps were set at Applecross from 25th August to 5th September, 1957 ; 7th to 13th August, 1958 ; 8th to 14th August, 1959, and 30th July to 5th August, 1960.

A field by Hartfield Wood (Grid ref. : 714463) consisted almost exclusively of *Molinia caerulea* Moench. with a small amount of bracken (*Pteridium aquilinum* (L.) Kuhn.). Hartfield Wood (Grid ref. : 716463) was predominantly a mixture of pine (*Pinus sylvestris* L.) and larch (*Larix decidua* Mill.) with occasional hawthorn (*Crataegus monogyna* Jacq.) and rowan (*Sorbus aucuparia* L.). The herb layer was sparse although some bracken was present. The trees were tall and old ; some had fallen and others felled. Traps were set under the thicker canopy and in scrub at the southern edge of the wood. Here, the vegetation consisted of rhododendrons (*Rhododendron* sp.), bracken, bramble (*Rubus* sp.) and *Molinia*. Traps were set along a moss-covered, dry-stone wall in a planted deciduous wood (Grid ref. : 720453). The commoner trees were birch (*Betula* sp.), beech (*Fagus sylvatica* L.), alder (*Alnus glutinosa* Gaertn.), ash (*Fraxinus excelsior* L.), hawthorn, willow (*Salix cinerea* L.), rowan and hazel (*Corylus avellana* L.). The herbs were represented by *Cynosurus cristatus* L., *Festuca* sp., *Holcus mollis* L., *Juncus* sp., *Moehringia trinervia* (L.), *Prunella vulgaris* L., *Pyrola minor* L., *Senecio jacobaea* L., *Succisa pratensis* Moench., *Trifolium* (?) *repens* L. and *Veronica montana* L. Traps were also set in rhododendrons along one of the drives in this wood.

In farmland traps were placed by dry-stone walls (Grid ref. : 716440). Oats, hay and root vegetables were all grown in the fields during the survey period. Separating the crops from the wall was a border containing a mixture of *Bellis perennis* L., *Centaurea nigra* L., *Heracleum sphondylium* L., *Plantago lanceolata* L., *P. major* L., *Potentilla anserina* L., *Prunella vulgaris*, *Pteridium aquilinum*, *Ranunculus acris* L., *Senecio jacobaea*, *Silene* sp., *Urtica dioica* L., *Viola cracca* L. and various grasses.

Traps were set at three elevations on the moorland viz. just over 300ft. (Grid ref. : 717438), about 400ft and on the western shore of Loch na Larach at about 900ft. (Grid ref. : 726433). The lowest trappings were made by a

wall ; here the vegetation included *Achillea millefolium* L., *Agrostis tenuis* Sibth., *Cynosurus cristatus*, *Dactylis glomerata* L., *Festuca* sp., *Galium hercynicum* Weig., *Plantago lanceolata*, *Prunella vulgaris*, *Pteridium aquilinum*, *Ranunculus* sp., *Rumex acetosa* L., *Senecio jacobaea*, *Trifolium repens* L. and a small quantity of *Calluna vulgaris* (L.). As the hill was ascended, *Calluna* became progressively denser until at Loch na Larach it dominated the vegetation. The trappings at 400ft. were made along a stone wall which had become almost completely covered by vegetation. At Loch na Larach traps were only set for two nights in 1957 and the results not included in Table 5. In Twenty-six trap nights two *Apodemus* and one *S. minutus* were caught.

Apodemus was apparently numerous and the most widespread of the small mammals having been recorded from every habitat surveyed. It was abundant in the deciduous wood but not so common in the coniferous wood and moorland. *Clethrionomys* favoured the woodland and scrub habitats and in Hartfield Wood was caught more often than the mouse. In the farmland and moorland it was occasional. *Sorex araneus* was ubiquitous but never frequent. *Microtus* was trapped in small numbers in the scrub at Hartfield and all the remaining habitats.

Laga

A small strip of wood occurs on the steep slopes of Allt Mor immediately north of where the burn passes under the Salen-Kilchoan road in Ardnamurchan parish (Grid ref. : 623612). The wood is about 100 yards from east to west. To the west it was flanked by pasture and on the east by arable land. Hazel was the dominant tree with birch and holly (*Ilex aquifolium* L.) also present. The herb layer was not dense and was represented by *Blechnum spicant* (L.) Roth., *Brachypodium sylvaticum* (Huds.) Beauv., *Deschampsia caespitosa* (L.) Beauv., *Endymion nonscriptus* (L.) Garcke, *Geum urbanum* L., *Stellaria nemorum* L., *Veronica* sp. and *Viola riviniana* Rchb.

Traps were set from 9th to 12th September, 1958 and from 2nd to 5th August, 1959. In the wood the lines were laid parallel to the burn. To the west of the wood they were set along a broken dyke in open pasture. No animals were caught here but elsewhere, where cover was good, *Apodemus* and *Clethrionomys* were plentiful.

Fearnoch Forest

The survey was conducted in and around Fearnoch Forest, Taynuilt, Argyllshire, from 22nd April to 5th May, 1958. These were the only spring trappings on the mainland. Three main habitats were trapped viz. : a Sitka spruce (*Picea sitchensis* (Bong.) Carr) wood, an adjoining area of *Calluna* and *Molinia* (Grid ref. : 974303) and a birch-rowan-oak wood (Grid ref. : 983304). Patches of dense spruce wood were devoid of a herb layer. Elsewhere, much of the ground was covered by a mixture of trees and undergrowth of *Molinia*, bracken, *Calluna* and *Sphagnum*. The oak-birch-rowan wood was open and the trees small. The floor was largely covered by *Molinia* with *Anemone nemorosa* L., *Calluna*, *Primula vulgaris* Huds. and, in the wetter places, *Myrica gale* L. These habitats lie 250–300ft. above sea level. When examined the dead grass was the main cover.

The small number of rodents (Tables 2, 3 and 5) collected suggests that, although Fearnoch was visited at a time of year when populations are likely to be low, they were not numerous in the habitats investigated. As *Molinia* covered much of the ground it appears that this plant may have an important role in determining the abundance and the species present. Shrews were common.

TRAPPINGS IN THE INNER HEBRIDES

Island of Mull

On the Island of Mull various types of habitat were trapped in the vicinity of Salen from 5th to 14th May and 2nd to 8th September, 1958 and 2nd to 9th July, 1959. They included a mixed deciduous wood (Grid ref. : 568433) and close to it, a similar but more open wood, arable land (Grid ref. : 553452), *Molinia* grassland (Grid ref. : 552453) and young spruce woodland (Grid ref. : 551454).

The mixed wood contained a large quantity of oak (*Quercus* sp.), but beech (*Fagus sylvatica* L.), ash, willow and birch were also present. There was not a thick herb layer and rock exposures were common. *Dryopteris filix-mas* (L.) Schott. was plentiful, *Juncus* sp. patchy and *Festuca* sp. and *Holcus mollis* thinly distributed. The open wood contained little oak and although hazel, ash, birch and willow were present, trees were generally less numerous. The herbage was denser and included *Blechnum spicant*, *Dactylis glomerata*, *Endymion nonscriptus*, *Festuca* sp., *Juncus* sp. and *Poa* sp. Traps were set along a dry-stone wall bordering a hay field. Some of the *Molinia* grassland contained young larch ; as the *Molinia* was dense and the trees widely spaced the results of these trapping have been included in Table 5. A stand of sitka spruce with a layer of bracken and *Potentilla erecta* (L.) Rausch. beneath it, was situated just within the boundary of Salen Forest.

Apodemus and *Clethrionomys* were ubiquitous and the latter most numerous in the deciduous and coniferous woods. The field mouse was commonest in the deciduous wood and agricultural land and *Microtus* in *Molinia* and spruce. Most *S. araneus* were caught in *Molinia* and arable land. In woods *Neomys* was within very short distances of burns and the individual taken in the *Molinia* was within 100–200 yards of the nearest water. The relative abundance and distribution of small mammals appears very similar on Mull to that on the mainland.

Island of Raasay

On the Island of Raasay the available vegetation types in the vicinity of Clachan were agricultural land, coniferous wood and associated scrub. Scrub (Grid ref. : 552367) immediately south of Home Loch consisted of thick undergrowth containing bramble, rhododendron, raspberry (*Rubus idaeus* L.), bracken and various grasses. Adjoining this was the scrub within the boundary of Borodale Wood (Grid ref. : 552366) which was more heathy in character. Spruce, occasional birch and alder, *Carex* spp., *Erica* spp., *Molinia*, *Calluna*, *Rubus idaeus*, small rhododendron, *Potentilla* sp., *Myrica gale*, *Cladonia* sp.,

Sphagnum and some grasses were present. Within the wood the trees were mostly old pines with a few spruce and alder. Rhododendrons were common. Traps were set along dry-stone walls flanking pasture (Grid ref. : 551365) and a field of cut hay (Grid ref. : 550363).

In the habitats examined *Clethrionomys* was particularly common. At Applecross, coniferous wood and associated scrub were also favoured by *Clethrionomys*. By comparison *Apodemus* was rather sparse and it is surprising it was not encountered more frequently in the agricultural land. *Sorex* was widespread and quite numerous.

Island of South Rona

South Rona is a small, uninhabited island. Large areas consist of moorland although a small planted, mixed (predominantly deciduous) wood occurs to the west. When the island was visited from 30th July to 5th August, 1958 the following trees were noted in the wood : birch, pine, rowan, oak, beech and lime (*Tilia* x *vulgaris* Hayne). The herbs included, *Blechnum spicant*, *Calluna*, *Corydalis claviculata* (L.) DC, *Dryopteris filix-mas*, *Erica tetralix* L., *Galium hercynicum*, *Molinia*, *Oxalis acetosella* L., *Potentilla erecta*, *Prunella vulgaris* and *Pteridium aquilinum*. The moorland traps were set in bracken, *Molinia*, *Calluna* and *Erica* and along dry-stone walls traversing the moors. They were also set in and around several of the derelict buildings at Big Harbour and Dry Harbour. A small patch of birch scrub was trapped at Big Harbour. The detailed location of the trap sites are given by Delany & Copland (1960) together with the total catch of small mammals. The present analysis does not include as many trap nights as only the traps set in one place for three nights have been included.

The most striking features are the very low overall catch of mammals and the complete absence from the mixed wood. The animals recorded in Table 2 were caught in the birch scrub.

Island of Rhum

In the immediate vicinity of Kinloch (Grid ref. : 402995) is as wide a variety of vegetation as can be found on the whole island. Mixed woodland, consisting predominantly of pine and sycamore but also including larch, birch, ash, alder and rowan occurred to the west and south of Kinloch Castle whilst to the north was arable land. Encircling the wood and farmland were moor and sea. The woodland floor was variable ; in places rhododendrons were numerous whilst in local patches of dense pine other vegetation was negligible. Traps were not set in the latter situation but in rhododendrons and mixtures of rhododendron, bramble, grasses, *Ranunculus* sp. and fallen timber. *Molinia* was trapped as well as the boundary of a field of oats. The traps were set between 27th and 31st July, 1959. Both species of mammal were present in small numbers.

Island of Colonsay

In the vicinity of Kiloran traps were set, between 18th and 27th August, 1959, in a mixed wood, grass moor, oak-birch wood and in fields. The mixed

wood (Grid ref. : 396966) contained sycamore, beech, oak, alder and lime. Nowhere where traps were set was the undergrowth dense although in addition to grasses it included, bramble, *Asplenium* sp., *Dryopteris filix-mas*, *Endymion nonscriptus*, *Heracleum sphondylium*, *Lonicera periclymenum* L., *Oxalis acetosella*, *Primula vulgaris*, *Teucrium scorodonia* L. and a little rhododendron. Although conifers were present, the places trapped were predominantly deciduous. To the east was an oak-birch wood (Grid ref. : 408966) which also contained rowan, hazel and willow. The floor was covered by bracken and grass. The trees were short and stumpy and the cover they afforded was not dense. Between the two woods lay stretches of *Festuca* grassland ; traps were set by walls across this grassland. Walls enclosing fields of oats (Grid refs. : 393970, 398974, 401973) were examined. Most *Apodemus* were caught in the mixed wood and by walls bordering the fields of oats. *Mus* was found in arable land at distances up to half a mile from the nearest buildings.

TRAPPINGS IN THE OUTER HEBRIDES

The Outer Hebrides is a group of bare, windswept islands much of whose area is covered by lochs, peat and wet moorland. A few small woods occur on Lewis and Barra. The machair provides stretches of arable land on the four main islands. It covers a small proportion of the total land area and is particularly sparse on Lewis (Darling, 1955). Several habitats examined appeared to be without a small mammal population. Furthermore, from the 1958 and 1959 trappings it was apparent that where mammals occurred they were in small numbers. The low catches after the first night (less than 1 per cent) and the resultant loss of trapping time prompted the more frequent moving of the traps in 1960. Consequently, in Tables 2 to 5 only the first nights trappings have been considered.

Island of Lewis

During two visits to Lewis from 15th to 28th August, 1958 and from 13th to 21st September, 1960 three localities were visited. At Balallan traps were set in a small plantation of pine and spruce (Grid ref. : 300215). Between the stands were patches of dense *Molinia*, *Calluna* and *Erica* and as the whole area was well fenced no sheep or cattle grazing had taken place. There was no catch from the traps in this wood. Traps were also set to the north of Loch Erisort around Valtos House (Grid ref. : 318206). They were placed by dry-stone walls surrounding fields of oats, hay and pasture. One *Apodemus* was caught.

In the grounds of Lews Castle, Stornoway (Grid ref. : 416327) a planted wood contained a mixture of larch, sycamore, oak, spruce, beech, rowan, copper beech, birch, pine, ash, chestnut (*Castanea sativa* Mill.), hawthorn and cypress (*Cupressus macrocarpa* Gord.). Also present were some vast banks of rhododendrons. Traps were set in the rhododendrons and in places where the tree or shrub cover was not at its densest. A scrub containing fallen timber, tree stumps, short rhododendrons, some *Juncus* sp. and *Digitalis purpurea* L. ; an embankment of rhododendrons and bracken and another of occasional

beech and bracken were examined. Only the scrub produced a catch of small mammals. When retrapped in 1960 none were caught.

Apart from an oatfield at Goathill Farm, Stornoway (Grid ref. : 437336) which caught two *Mus*, the remaining traps were set in 1960, at Barvas (Grid ref. : 357512). Here, a stretch of arable land possessed to its west one of the few strips of machair on Lewis. The arable land was subdivided into very small patches of oats, potatoes and hay. Traps were placed by patches of these three crops, in some instances alongside and in others remote from dry-stone walls. Both *Apodemus* and *Mus* were caught. Further west on the machair the vegetation was thin. *Ammophila arenaria* (L.) Link was present and large areas were covered by butterbur (*Petasites* sp.). It was in the latter that *Apodemus* was caught most frequently.

On Lewis and Harris *Apodemus* is widespread for in addition to the above records Elton (1933) caught animals in other parts of Stornoway, material exists in the British Museum (Nat. Hist.) from Callernish and Uig and Barrett-Hamilton & Hinton (1910–21) refer to animals from the Butt of Lewis and Tarbert, Harris. It is apparently not numerous in any locality. In August, 1933, Elton caught it much less frequently than *Mus*.

Island of North Uist

Traps were set on arable land, some of which was machair, and the adjoining moorland at Newton Ferry (Grid ref. : 886772) from 30th August to 8th September, 1960. A large proportion of the traps were placed in oats and rye which were the main crops. They were in small patches and near ready for harvesting. The vegetation around them consisted of *Achillea millefolium* L., *Anthyllis vulneraria* L., *Avena fatua* L., *Centaurea nigra* L., *Chrysanthemum segetum* L., *Daucus carota* L., *Equisetum arvense* L., *Euphorbia peplus* L., *Euphrasia* sp., *Holcus lanatus* L., *Linum catharticum* L., *Lithospermum arvense* L., *Lotus corniculatus* L., *Melampyrum pratense* L., *Myosotis* sp., *Plantago lanceolata*, *Polygonum* sp., *Raphanus raphanistrum* L., *Rhinanthus* sp., *Senecio jacobaea*, *Sinapis arvensis* L., *Thalictrum minus* L. and *Viola lutea* Huds. Only on one occasion was a row of ten traps set in a field of rye the day after cutting ; a similar row was set in oats. On wet ground stands of *Phragmites* sp. contained *Caltha palustris* L., *Filipendula ulmaria* (L.) Maxim., *Holcus lanatus*, *Potentilla anserina* and *Vicia* sp. A dry-stone wall to the east of the main north-south road, flanked sheep-grazed grass and heather moor. Traps were set along this wall as well as in the arable land and *Phragmites*. *Microtus* and *Mus* were present through the area. *Apodemus* did not favour the moorland and was present in comparatively small numbers in the arable land (Table 4).

Island of South Uist

On South Uist, between 18th and 24th July, 1959, 20th and 29th August, and 8th and 12th September, 1960 traps were set over an extensive area and within two main types of vegetation. They were the agricultural land at Grogarry and Askernish and the adjacent moorland. On the moors sixty-nine traps were set in derelict buildings and were not placed in lines. The moors at Druidibeg (Grid ref. : 795385) and on the slopes of Triuirebheinn (Grid

ref. : 805214) were covered by *Calluna* which was short at the former and 1 to 2 feet, tall at the latter. Some rhododendrons were present at Druidibeg. At Auratote (Grid ref. : 792206) and around Loch Boisdale (Grid refs. : 788195, 795202) the moor was mainly *Festuca* grassland frequently covered by bracken.

At Grogarry, a large field containing a mixture of oats and barley (Grid ref. : 761398) was situated on machair. Further inland were several fields of closely grazed pasture (Grid ref. : 765398). Traps were set in a small patch of potatoes at Stilligary (Grid ref. : 768384). The hayfields and pastures at Askernish (Grid ref. : 734239) were low-lying and inclined to be wet with *Phragmites* bordering one of the fields. Apart from grasses the remaining vegetation consisted mainly of *Centaurea nigra*, *Iris pseudacorus* L. and *Potentilla anserina*.

Small mammals were of restricted distribution and limited numbers. *Mus* was established in fields at Grogarry and Askernish. Of the six main walls along which traps were set in the pastures at Grogarry *Apodemus* was only caught along one and was not caught at Askernish. It was also taken in oats on the machair and amongst the remains of buildings at Auratote. The negative catch from this habitat in 1960 may have been due to the introduction of brown rats (*Rattus norvegicus* (Erxl.)) one of which was caught in a trap. In 1959 three *Microtus* and one *S. minutus* were caught around Loch Boisdale but have not been included in Table 5 as they were not caught on the first trap night.

Island of Barra

On Barra the survey was conducted at North Bay (Grid ref. : 711025) from 11th to 17th July, 1959 and at Vaslain (Grid ref. : 693057) from 11th to 19th August, 1960. At North Bay the edges of unwalled hayfields, a small potato patch, dry-stone walls by a scrub (formerly a garden) with bracken, gorse and bramble dominating the vegetation, were examined. In the small wood (Grid ref. : 702033) sycamore was dominant and spanish chestnut, *Prunus* sp., spruce, fir (*Abies alba* Mill.), willow and gorse present. The herbs were *Aegopodium podagraria* L., *Agrostis stolonifera* L., *Anthoxanthum odoratum* L., *Blechnum spicant*, *Deschampsia caespitosa*, *D. flexuosa* (L.) Trin., *Holcus lanatus* L., *Iris pseudacorus*, *Juncus* sp., *Lapsana communis* L., *Leontodon* (?) *hispidus* L., *Luzula multiflora* (Retz.) Lej., *Orchis* sp., *Plantago lanceolata*, *Potentilla reptans* L., *Prunella vulgaris*, *Pteridium aquilinum*, *Rubus* sp., *Rumex acetosa* L., *Senecio aquaticus* Hill, *Urtica dioica* and *Viola riviniana*.

At Vaslain a stretch of low-lying land contained vegetation similar to that at Newton Ferry. Patches of *Phragmites* 6 to 7 feet tall covered the low wet ground and were accompanied by *Anthoxanthum odoratum*, *Caltha palustris*, *Centaurea nigra*, *Juncus* sp., *Gentianella campestris* (L.), *Mentha* sp., *Menyanthes trifoliata* L., *Molinia caerulea*, *Narthecium ossifragum* (L.) Huds., *Pedicularis palustris* L., *Potentilla anserina*, *P. erecta*, *Senecio jacobaea*, *Succia pratensis* and *Trifolium pratense* L. The slightly higher ground was dryer and more sandy and on this the main crops were rye, oats, barley and potatoes. Traps were set in all these crops as well as the *Phragmites*.

Apodemus was widespread at Vaslain and most frequent in the rye. At North Bay, a small number were trapped in the wood in 1959 but none in 1960. Two pygmy shrews were trapped here in 1959 but on trap nights excluded from the figures in Table 2. Both *Mus* and *Apodemus* had previously been reported from Vaslain (Warwick 1938). From the fields and scrub at North Bay, *Apodemus* appears to be absent.

DISCUSSION

In comparing numerical data it has been recognized that the figures only give an approximate index of relative abundance as trapping success may be subject to variation. There are nevertheless some features of dissimilarity between the small mammal faunas on the islands and the mainland.

In the Inner Hebrides the ecological situation on the Island of Mull appears similar to that on the mainland both as regards the habitats occupied by the small mammals and the relative numbers in each. In 1957, on Raasay *Clethrionomys* appeared to be as numerous, and *S. araneus* rather more so, as on the mainland. With the exception of Mull, the Inner Isles showed a general decline in the numbers of *Apodemus*, this being most noticeable in the deciduous woods and the agricultural land.

The distribution of small mammals was similar in each of the Outer Isles and agrees with that found by Elton (1938) on the Island of Pabbay. Established populations of *Mus*, *Apodemus* and on the Uists, *Microtus* occurred on the machair and adjoining arable land ; *Apodemus* was present in the woodland; *S. minutus* occurred widely in very small numbers and *Microtus* was also found on the moorland. The catch of *Apodemus* on machair was invariably lower than on the arable land at Applecross (Table 4).

Apodemus was common and ubiquitous on the mainland and the Island of Mull. On the remaining islands it was of restricted distribution and apparently smaller numbers. The reasons for these differences are not clearly understood. The possibility of trapping on an island in a year of low numbers cannot be precluded although it appears unlikely that so many of the visits should have coincided with bad years. Furthermore, there is no indication from the Applecross trappings that *Apodemus* experienced a year of markedly low numbers between 1957 and 1960. The field-mouse is an omnivore capable of subsisting on a wide variety of food (Barrett-Hamilton & Hinton, 1910–21 ; Miller, 1954 ; Kikkawa, 1959) although it is possible that in spite of this adaptability, winter food may be scarce in more exposed situations. In winter, some islands are probably more exposed to adverse weather than the mainland. The agricultural land, including the machair, in the absence of crops, with the herbs dead and close to the ground and with many low-lying areas waterlogged must offer an unfavourable habitat and a poor food source. The moorland and leafless woodlands would be equally arid. In contrast, many trappings on Raasay and Colonsay were in more sheltered situations and it is surprising that the arable land on the latter island did not yield a larger catch.

Apodemus appears to prefer a habitat with a firm dry substrate (where herbs are not dense) over which it can wander widely and rapidly and that offers

cover suitable for nesting and concealment. The importance of the physical habitat is illustrated by Boyd's (1959) trappings on the very exposed island of Hirta, St. Kilda. Here the field-mice were very common. Also present were hundreds of disused, dry-stone storage chambers (cleitean) and it was in these that many mice were caught. No cleitean were observed in the present survey and in their absence the dry-stone wall was the only permanent cover although in some places e.g. Vaslain, they were absent.

Although Southern & Laurie (1946) found *Mus* and *Apodemus* resident all the year round in fields in the Oxford district Williamson & Boyd (1960) observed that with the disappearance of man e.g. St. Kilda, *Mus* is unable to compete successfully with *Apodemus*. It appears that a field population of *Mus* is either directly or indirectly dependent on the presence of man. On the Outer Hebrides the winter populations of both species of mice are probably very reduced, competition is at a maximum and it is possibly at this time that the main reservoir of house mice is in human habitations. The numerous new habitats available in spring could then be entered by both species whose general sparsity may tend to reduce intense competition.

Microtus was widespread and found in small numbers in all four habitat types. Unlike *Apodemus*, there is little evidence of numbers declining in the Outer Hebrides where the problem of winter survival probably affects this species less. There were indications from its occurrence in wet grasslands at Salen, Mull and wet meadows at Askernish, South Uist that it will tolerate slightly wetter situations than *Apodemus*.

In the absence of *S. araneus*, *S. minutus* did not become markedly more numerous. Everywhere it was uncommon. On Colonsay and Rhum, from which the former is absent, four pygmy shrews were caught in 600 trap nights whilst on the Outer Isles, using a more rigorous trapping technique, two were caught in 1624 trap nights. Three were caught in 1217 trap nights on South Rona, Raasay and Mull (summer trappings only). These figures represent the generally low overall successes of 0·5 per cent, 0·12 per cent and 0·25 per cent, respectively. Were *S. minutus* filling the niche, on Rhum, Colonsay and the Outer Hebrides, that was occupied by *S. araneus* in other places, it could be expected in greater numbers.

Predatory species were less numerous on the islands than the mainland. Weasel, stoat, fox, wild cat, feral cat and possibly pine marten were recorded from Applecross at the time of the survey. The feral cat was present on all the islands except South Rona and in addition, on Mull, there were polecat-ferrets and stoats. Weasels were present on Raasay. Of the birds, buzzards were common except on the Outer Hebrides where they were less frequent ; the kestrel was ubiquitous but not abundant and the short-eared owl is recorded as nesting regularly in the Outer and infrequently in the Inner Hebrides (Witherby *et al.*, 1949). From these data there appears little indication of heavier predator pressure on the islands.

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SUMMARY

1. Spring and summer collections of small mammals, using Longworth traps, were made from 1957 to 1960 at Applecross, Laga and Taynuilt and on the Islands of South Rona, Raasay, Rhum, Mull, Colonsay, Lewis, North Uist, South Uist and Barra.

2. *Sorex araneus*, *S. minutus*, *Neomys fodiens*, *Apodemus sylvaticus*, *Clethrionomys glareolus*, *Microtus agrestis* and *Mus musculus* were present on the mainland although *Mus* was not trapped. With the exception of Mull the islands lacked one or more of these species. Various vegetation types have been examined and attempts made to compare their small mammal faunas.

3. Coniferous and deciduous woods, moorland and agricultural land were trapped at Applecross every August of the survey. *Apodemus* and *Clethrionomys* were the commonest species. The former was widespread and most abundant in the deciduous wood and the agricultural land whilst the latter was most common in woodland. *S. araneus* and *Microtus* were widespread but not abundant. Trappings elsewhere on the mainland supported the findings at Applecross.

4. Trappings in woods, grassland and agricultural land on the Island of Mull in May, July and September suggest that the numbers and distribution of mammals were similar to those on the mainland.

5. On Raasay, *Clethrionomys* was generally abundant in the habitats available (coniferous wood and agricultural land) although *Apodemus* appeared less numerous than on the mainland. This infrequency of *Apodemus* was generally encountered on the remaining islands. Woods and moors were examined on South Rona, Rhum and Colonsay in addition to agricultural land on the latter two islands.

6. On the Outer Hebrides suitable small mammal habitat was sparse. *Apodemus* was caught in woodland on Barra and Lewis and on machair on all the islands. Occasional records were obtained from moorland. It was not numerous and nowhere did numbers attain the highest totals on the mainland. *Microtus* was widespread on the Uists and most common on the machair. Although *Mus* was common in agricultural land on the Outer Isles the only catches elsewhere in the survey were on Colonsay.

7. *Sorex minutus* was present on every island but no more abundant on those from which *S. araneus* was absent. It was trapped in very small numbers. *Neomys* was only present on Raasay and Mull and usually near water.

8. The absence of certain species does not appear to result in any numerical increase in those remaining but rather an overall decline as the terrain becomes progressively less compromising.

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OBSERVATIONS ON THE DIGESTIVE ENZYMES AND CELLULOLYTIC BACTERIA OF THE GIANT LAND SNAIL *ACHATINA FULICA* AND THEIR OCCURRENCE IN THE GASTROPODA

BY

KRISHNA CHANDRA GHOSE

Zoology Department, City College, Calcutta

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The digestive enzymes and the cellulolytic bacteria in the gut of *Achatina fulica* have been investigated. Amylase is present in saliva, gastric juice, intestine, digestive gland and in small amounts in the stomach and rectum. Protease is present in gastric juice, stomach, intestine and digestive gland. Saliva and rectum contain traces of protease. Lipase is present in gastric juice, stomach, intestine, rectum and digestive gland but not in saliva. Cellulase is slightly present in digestive gland alone. Cellulolytic bacteria are present in intestine.

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INTRODUCTION

Many workers have investigated the digestive enzymes of the gastropod molluscs but much remains to be done before the significance of the differences which occur in various members of the class can be appreciated. The results are presented in this paper of an investigation of the digestive enzymes of the giant land snail, *Achatina fulica*. The cellulolytic bacteria, however, have been studied only in a few molluscs.

METHODS AND RESULTS

ENZYMES

Snails were dissected on trays containing ice. Samples of saliva and gastric juice were collected and portions of the stomach, intestine, rectum and digestive gland were taken and placed in test tubes, which were kept in a beaker containing ice to arrest any enzymatic activity.

Extracts of the stomach, intestine, rectum and digestive gland were made by grinding 1 grm. of the tissue in a mortar with sea sand and 5 ml. of chilled

glycerol. The extracts were kept in a refrigerator for twenty-four hours and then centrifuged, the supernatant fluid, to which was added a few drops of toluene, being used as the enzyme extract. Boiled extracts were used in the control experiments.

Amylase

One ml. of 1 per cent starch solution plus 2 ml. of phosphate buffer of pH 6·2 were used as the substrate. The mixture was incubated with 0·5 ml. of the glycerol extract at 36°C for sixteen hours. Absence of a reaction with iodine and the reduction of Benedict's solution indicated a positive result. The results are shown in Table 1.

Table 1—Amylolytic activity as determined by iodine and Benedict's test.

Fluid or	Iodine test		Benedict's test		
Tissue	Experiment	Control	Experiment	Control	Conclusion
Saliva	Positive	Negative	Positive	Negative	++
Gastric Juice	Positive	Negative	Positive	Negative	++
Stomach	Slightly positive	Negative	Positive	Negative	+
Intestine	Positive	Negative	Positive	Negative	++
Rectum	Slightly positive	Negative	Slightly positive	Negative	+
Digestive gland	Positive	Negative	Positive	Negative	++

++ = Prominent amylolytic activity
+ = Little amylolytic activity

Table 2—Proteolytic activity as determined by Biuret test.

Fluid or tissue	Experiment	Control	Conclusion
Saliva	Slightly positive	Negative	+
Gastric juice	Positive	Negative	++
Stomach	Positive	Negative	++
Intestine	Positive	Negative	++
Rectum	Slightly positive	Negative	+
Digestive gland	Positive	Negative	++

++ = Prominent proteolytic activity
+ = Little proteolytic activity

Protease

Two ml. of phosphate buffer solution of pH 7·2 were put into a test tube and 0·5 ml. of the glycerol extract and 2 ml. of 1 per cent casein solution were added. The mixture was incubated for sixteen hours at 36°C. Hydrolysis of protein was measured by the Biuret test and the results are shown in Table 2.

Lipase

To ten drops of pure olive oil 2 ml. of phosphate buffer solution of pH 7·0, 0·5 ml. of 5 per cent solution of sodium tauroglycocholate and two drops of toluene were added. The mixture was incubated with 0·5 ml. of the glycerol extract at 36°C for sixteen hours. Lipolytic activity was determined by titrating the free acids of both the control and experiment with 0·1 N NaOH using phenolphthalein as an indicator and the results are shown in Table 3.

Table 3—Lipolytic activity as determined by titrating the free acids with 0·1 N NaOH.

Fluid or tissue	Ml. of 0·1 N NaOH required to titrate the free acids		Difference in ml. of 0·1 N NaOH required for the neutralization of free acids in control and experiment.	Conclusion
	Experiment	Control		
Saliva	1·05	1·05	0·00	−
Gastric Juice	1·30	1·10	0·20	++
Stomach	1·54	1·52	0·02	+
Intestine	1·80	1·36	0·44	++
Rectum	1·84	1·78	0·06	+
Digestive gland	1·98	1·45	0·53	+++

− = Absence of lipase
+ = Little lipolytic activity
++ = Prominent lipolytic activity
+++ = Maximum lipolytic activity

Cellulase

Measured quantity of cellulose powder (200 mesh) was added to 2 ml. of phosphate buffer solution of pH 5·8 and 0·5 ml. of the glycerol extract, and incubated for twenty-four hours at 36°C. Benedict's solution was used to test for the presence of reducing sugars. The results are shown in Table 4.

Cellulolytic bacteria

To study the growth of cellulose-decomposing bacteria from the gut, inocula were prepared from the washings of the crop, stomach, intestine and rectum and also from intestinal and rectal contents.* Filter paper and Dubos' medium were used in tests.

The medium was distributed in culture tubes containing strips of filter paper four inches long and half an inch wide. The inoculum was suspended in 10 C.C. of sterile water and each tube of liquid medium received 1 C.C. inoculum. They were incubated at 30°C. and results were recorded at intervals of seven days.

Table 4—Cellulolytic activity as determined by Benedict's test.

Fluid or tissue	Experiment	Control	Conclusion
Saliva	Negative	Negative	—
Gastric juice	Negative	Negative	—
Stomach	Negative	Negative	—
Intestine	Negative	Negative	—
Rectum	Negative	Negative	—
Digestive gland	Positive	Negative	+

— = Absence of cellulase
+ = Little cellulolytic activity.

The appearance of bacteria on filter paper strips was shown by straw-yellow and dark-yellow spots at the liquid level. Being shaken vigorously, filter paper strip breaks along this line. The cultures were transferred to fresh media and grown in subcultures for the second generation.

Dubos' medium for cellulose bacteria

Sodium nitrate ($NaNo_3$)	0·5 grm.
Dipotassium phosphate (K_2HPO_4)	1·0 grm.
Magnesium sulphate ($MgSO_4 \cdot 7H_2O$)	0·5 grm.
Potassium chloride (KCL)	0·5 grm.
Ferric sulphate ($Fe_2(So_4)_3 \cdot 9H_2O$)	trace
Distilled water	1000·0 ml.
Reaction	pH 7·5

* A mucous string is always present in the intestine and rectum of a starved snail.

Aerobic series

Days of incubation, twenty-one days (five tubes of culture in each series). Temperature of incubation 30° ±2°C. Medium—(Dubos').

Bacterial strains examined from lot five and six belong to the family cytophagaceae. They are strictly aerobes. Optimum temperature 28°–30°C.

Rods Gram-negative—occurring singly and wide at the centre. Length 3–5μ.

Stained with difficulty. Identified as *Cytophaga hutchinsonii*. The bacterial cultures isolated from lot three are probably a variant of the above lot. They differ from *Cytophaga hutchinsonii*.

Inoculum	Particulars of Inoculum	Bacterial growth on filter paper strip				
1	Crop	0	0	0	0	0
2	Stomach	0	0	0	0	0
3	Intestine	+	+	+	+	+
4	Rectum	0	0	0	0	0
5	Intestinal content	+	+	+	+	+
6	Rectal content	+	+	+	0	0

+ = Positive growth.

DISCUSSION

The digestive enzymes, viz. amylase, protease, lipase and cellulase were studied in saliva, gastric juice, stomach, intestine, rectum and digestive gland. All were found to be present, though in varying degrees.

From the above experiments it becomes evident that the digestion of carbohydrates starts when the food comes in contact with saliva and gastric juice respectively. Proteolytic and amylolytic activities were observed in all juices and tissues under experiment, and this suggests that the food of the animal may consist of protein and carbohydrate mainly and that digestion is initiated by saliva and completed in the rectum.

The presence of amylase, protease, lipase (maximum amount) and cellulase in the digestive gland indicates the digestive functions of the secretion of this gland, in contrast to the liver of vertebrates, or it may be that stored food materials, e.g. carbohydrate, fat and protein present in the digestive gland are mobilised by the action of these enzymes when required (e.g. starvation). The pronounced lipolytic activity of the digestive gland suggests that the digestion of fat in the animal principally depends on the secretion of this gland.

In *Achatina*, the secretion of the posterior lobe of the digestive gland is discharged into the stomach and it is likely that the greater amylolytic and lipolytic activity of the gastric juice when compared with extracts of the stomach wall is due to the presence of digestive gland secretion in the lumen of the stomach.

Cellulase, which directly converts cellulose into sugar, has been traced in the majority of gastropods—*Helix* (Karrer & Illing, 1925), *Pterocera* (Yonge, 1932), *Limax* (Tribby & Carmichael, 1935) and it is active particularly in Pulmonata (Stone & Morton, 1958). It is striking that cellulase is absent in *Onchidella* (Fretter, 1943) and is only slightly present in the digestive gland of *Achatina* though both of them are herbivorous. The deficit of cellulase in *Achatina*, in comparison with other gastropods, has possibly been compensated by the presence of cellulolytic bacteria in the intestine. Cellulolytic bacteria are absent in the rectum but the presence of the same in the rectal content suggests that the bacteria there have been carried over from the intestine. It is

interesting that *C. hutchinsonii* found in the intestinal content could not be traced in the washing of the intestine, and the variant of *C. hutchinsonii* obtained from the intestine were not found in the intestinal content. In *Achatina*, as in some other gastropods, a considerable proportion of the ingested plant food comes out undigested with the faecal matter but the present studies do not support the contention of Fretter that except for mechanical action the cell walls of the ingested plants are unaffected by their passage through the gut and only the contents of those cells, which have been opened are utilized. The powerful amylase present in *Helix* (Taylor, 1894 ; Krijgsman, 1928), and *Pterocera* (Yonge, 1932), is supposed to be secreted by the salivary gland but is widely distributed in *Achatina* and is present in all the fluids and tissues examined. Protease is absent in style-bearing molluscs and this is presumed to be compensated for by the liberation of soluble proteins from the cell-sap of plant food by the action of cellulase (Yonge, 1930). Protease is present in large amounts in carnivorous molluscs (Mendel & Bradley, 1905) and a powerful proteolytic activity was observed in the stomach, intestine and digestive gland of *Achatina*. It feeds on dead insects and snails and these are adequately digested by them. Plant material constitutes the bulk of the food but they also ingest animal material and the presence of a strong protease is possibly due to this ' mixed food ' habit. Little lipolytic activity has been found in *Helix* (Taylor, 1894) and *Pterocera* (1932), but pronounced in *Achatina*. In this animal, a considerable amount of fat is stored and presumably utilized during the prolonged aestivation period.

Various observations have been made regarding the rate of fat digestion in different molluscs but all workers are unanimous that the digestion of carbohydrates takes place rapidly in all herbivorous molluscs.

The presence of digestive enzymes in the rectum of *Achatina*, though in small quantities, is a phenomenon, which has not been reported from any other mollusc. The histology of the rectum, however, reveals the presence of fairly large multicellular glands embedded in the tissues of its wall.

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LIFE CYCLES OF FOUR FRESHWATER SNAILS IN LIMITED POPULATIONS IN LOCH LOMOND, WITH A DISCUSSION OF INFRASPECIFIC VARIATION

BY

W. RUSSELL HUNTER

Department of Zoology, University of Glasgow

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(With 10 figures in the text)

With dredged samples from an isolated bank in Loch Lomond providing standards, data are presented on the interpopulation variations in growth and reproduction which occur in five species of freshwater snails. Infraspecific differences between populations in *Planorbis albus* and *Valvata piscinalis* involve only growth rates and the time and intensity of the breeding season. In *Physa fontinalis*, *Lymnaea peregra* and *Ancylus fluviatilis*, interpopulation differences involve the seasonal course of the reproductive cycle (and the number of generations per year), as well as growth rates. A series of the known life cycles of freshwater pulmonates is then considered : two patterns of simple annual cycle, and two patterns each involving a second generation annually, are described, besides certain more exceptional life cycles. All four patterns have been found in different populations of *P. fontinalis* and *L. peregra*.

Variations in breeding are dependent both on environmental factors, water temperature being most important, and on endogenous causes involving the growth of the snails ; variation in mortality may involve environmental limitation. Most interpopulation variations can be environmentally evoked, but some differences seem genetically determined. It is suggested that adaptive plasticity, as found in several aspects of the physiology of these snails, is of fundamental selective value, given the temporal and spatial peculiarities of the freshwater environment.

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INTRODUCTION

Recent work on growth, reproductive rates, and life cycles in freshwater snails has revealed that considerable variation occurs from population to population within each species (see De Wit, 1955 ; De Witt, 1955 ; Duncan, 1959 ; Geldiay, 1956 ; Hunter, 1953 a, 1957, 1961). This infraspecific

variation involves the size attained by adult snails when they begin to breed, the season in which breeding occurs, and the life-span of each generation of snails. This present paper records data on growth and life cycles which were obtained by regular sampling of naturally limited populations of four species in Loch Lomond, and from comparative samples of the same species from other populations. The species concerned are the three pulmonate snails *Physa fontinalis* (L.), *Planorbis* (*Gyraulus*) *albus* Müller, *Lymnaea* (*Radix*) *peregra* (Müller), and the freshwater prosobranch *Valvata* (*Cincinna*) *piscinalis* (Müller). [Systematics and specific nomenclature used here follow those adopted in the most recent Census of the British non-marine Mollusca (Ellis, 1951) and approved by the International Commission on Zoological Nomenclature (*Opinions* 335, 336, and 363, 1955)]. In almost all cases, the comparative samples were taken contemporaneously with the standard ones from the limited populations in Loch Lomond, and thus the infraspecific interpopulation variations are not obscured by the year to year variations, the extent of which has already been described (Hunter, 1961). Data already published (Hunter, 1953 a ; Geldiay, 1956) on a fifth species, the pulmonate limpet, *Ancylus fluviatilis* Müller, are briefly reviewed and then discussed with those from the other species. All the pulmonate snails, and the one prosobranch *Valvata*, discussed, are hermaphrodite.

The results are utilized in a comparative discussion of the seasonal patterns of growth, overall growth rates, and period and intensity of breeding in the five species in different local populations, and on the environmental bases of such interpopulation (infraspecific) variation as occurs. There follows a more general discussion of adaptive plasticity in growth and reproduction, and in other aspects of the physiology of freshwater snails, and of the evolutionary significance of such plasticity. Some of the data in the present paper, and certain conclusions drawn from them, were discussed earlier, though then unpublished, at the meeting of the British Association in Glasgow in September 1958 (see short reports in Yonge, 1958 ; Haslett, 1958).

The work was carried out in the Department of Zoology, University of Glasgow, and at the Freshwater Laboratory, Glasgow University Field Station, Rossdhu, Loch Lomond ; and forms part of a series of investigations on the physiology and ecology of freshwater snails begun in 1948. All the regular samples and the greater part of the comparative ones were collected in the seasons 1952–54, and some preliminary measurements and work on this paper done in 1955. The entire material was re-measured in 1957–58 and final calculations and preparation of this paper were done in 1958–60.

SPECIES, METHODS, AND THE LIMITED POPULATIONS

To consider variability in growth and life cycle in different populations of freshwater snail species, a necessary basis is the collection of a regular series of standard samples for each species. For obvious reasons, the " best " standard populations for sampling are those as isolated yet as uniform as possible. Complications are involved in those populations with more than one period of reproduction in each year, and thus the standard populations have to be ones in which " poor " feeding conditions give low rates of growth and a single

annual breeding season. Lastly, the standard populations are best drawn from an environment in which the physical and chemical conditions vary little both diurnally and annually. Such relatively stable conditions are more readily met with offshore in large lakes than in smaller bodies of fresh water. Uniform snail populations of sufficient extent are also more readily found in the former environment. Obviously a snail population living on the bottom of a large lake in deep or moderately deep water could show most of the desired characteristics. In Loch Lomond, however, there are no gastropods found on the bottom silts of the profundal zone, i.e. from depths of about 22 m. downwards. Even in the sub-littoral zone (e.g. in depths of about 6 to 11 m.), the only snail found in any numbers is *Valvata piscinalis*. Fortunately, there are several offshore reefs and banks lying within a few metres of the surface. The faunas on these isolated banks commonly include four out of the fourteen species of freshwater snails known to occur in Loch Lomond (see Hunter, 1957). These four species, which are also the most ubiquitous in the inshore waters of Loch Lomond and elsewhere, are : *Physa fontinalis*, *Planorbis albus*, *Lymnaea peregra*, and *Valvata piscinalis*. The standard samples were collected from limited populations of these four species on the isolated offshore McDougall Bank. The only other freshwater snail at all abundant and ubiquitous in the West of Scotland is the pulmonate limpet, *Ancylus fluviatilis*. This fifth species is also discussed, but on data already published (Hunter, 1953 a ; Geldiay, 1956).

A single shell dimension for each species was used, as shown in Fig. 1. For the two turbinate-shelled species, *Physa fontinalis* and *Lymnaea peregra*, the standard dimension is the shell-length (SL), i.e. the maximum length of the shell from the apex of the spire to the peristome or outer edge of the aperture. For *Planorbis albus* and *Valvata macrostoma* the maximum diameter (MD) of the shell is used. This is the greatest transverse width, measured from the outer edge of the peristome across the umbilicus to the opposite periphery of the last or " body " whorl of the shell. As regards *Physa fontinalis* and *Planorbis albus*, other measurements have shown that shell shape does not vary greatly within the range of populations studied, and thus the single standard dimension is justifiable. Shell shape in *Lymnaea peregra* varies greatly, but the populations described in this paper are all of similar intermediate type, being neither extremely convex with reduced spire—form " *ampla* ", nor high-spired and elongate—form " *peregra* " (as classified in Hubendick, 1945, 1951). The shell form of *Valvata piscinalis* found in Loch Lomond is low-spired when compared with " typical " specimens from more eutrophic waters. The range of shape encountered in *Lymnaea* and *Valvata* will be further discussed. Data reported for *Ancylus fluviatilis* are based on measurements of detached periostraca in fluid (see Hunter, 1953 a, 1961), in which the aperture length (AL), the greatest dimension across the opening of the limpet-shell, was recorded.

McDougall Bank lies about 800 m. offshore from Rossdhu (Full National Grid Reference 26/365870). It has a " plateau " surface of nearly 1000 sq. m. lying about 2 m. below the lowest (drought) water level of the loch, although surrounded by water with depths of 8 to 13 m. below this level. The minimum

depth of water over the bank can range from 2·3 to 4·4 m. within any year. A transect profile of the bottom which includes this offshore bank has been given elsewhere (Hunter, 1953d—Fig. 1). The deposits vary from silty sands to fine gravel. These sands support a turf of *Isoetes lacustris*, and in places lusher stands of *Nitella opaca* and some *Potamogeton perfoliatus*. The fauna has been described and discussed by Weerekoon (1956 a-b). It is relatively poor both in numbers of species and in numbers of individual animals. The respiratory schesis of the populations of *Lymnaea peregra* and *Physa fontinalis* has been discussed elsewhere (Hunter, 1953 d). Feeding conditions are poor, and growth of all four species of snails is slow.

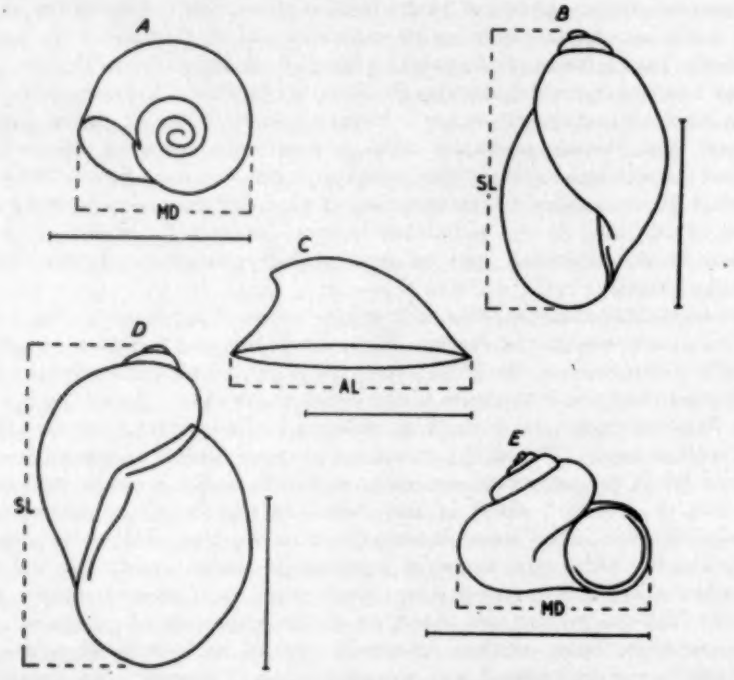

Fig. 1—The shells of the five species sampled, and standard dimensions measured. A : *Planorbis albus*, B : *Physa fontinalis*, C : *Ancylus fluviatilis*, D : *Lymnaea peregra*, and E : *Valvata piscinalis*. The black scale is five millimetres long in each case ; the broken line indicates the standard dimension (MD=maximum diameter, SL=shell length, and AL=aperture length). Other measurements used are discussed in the text.

The standard samples of snails were collected using a dredge with an inner bag of jute sackcloth and a frame opening of 20×50 cm., the biting edge being armed with 3·5×1·3 cm. teeth. Also, a few quantitative samples (see next section) were taken with a small weighted Petersen grab. The dredged material was taken ashore and sieved. The sieve was trough-shaped, 75×20×13 cm., made of wire gauze which passed much of the finer sand and all silt (maximum

opening in mesh=1·05 mm.). The minimum sizes of snails retained will be discussed later. Larger plant material was thoroughly washed and discarded when free of snails. The sieved residue was spread out on flat dishes and all snails individually picked out and sorted into species. This process usually yielded about 300 to 400 snails. Comparative samples of the four species were initially collected both from inshore waters of Loch Lomond and from elsewhere, but it became clear that the number of sample-series could be reduced. To anticipate results, interpopulation differences were found in rate of growth and in time of breeding for all four species—but differences in the number of generations per year were only found in *Lymnaea peregra* and *Physa fontinalis*. Accordingly, comparative samples forming complete annual series are presented only for these two latter species. For *Planorbis albus* and *Valvata*, single comparative samples taken from each population at its breeding season alone need be considered. The main series of comparative samples for *Physa fontinalis* was collected in the Loch Lomond littoral near the Field Station at a locality described elsewhere (Hunter, 1961—"New" sampling station at Rossdhu), and the main series for *Lymnaea peregra* from a pool in the adjacent river, the Fruin Water, which flows into Loch Lomond. For reasons discussed later, the inshore populations of *Lymnaea peregra* in Loch Lomond itself could not provide a suitable annual series of samples. These comparative samples of snails, with the exception of one sample of *Valvata* (dredged from Castle Loch, Lochmaben), were collected by hand from stony substrata.

All samples were sorted alive, fixed in either 10 per cent neutral formalin or 95 per cent alcohol, and stored and measured in 70 per cent alcohol. Larger snails were measured with an engineer's dial caliper; for smaller snails a microprojector was used. Measurements of much of the samples of *Planorbis albus* and *Valvata* were checked by being carried out by both methods. As the measurements were made, they were grouped in tenths of a millimetre (i.e. all shells between 4·15 mm. and 4·25 mm. were recorded in the interval whose class mark was 4·2 mm.). All samples of all four species were thus measured to intervals of 0·1 mm. In all standard and in most comparative samples, the original class marks were used subsequently for the calculations of means and standard deviations, and for the histograms in Figs. 3 to 8. In certain comparative samples of *Lymnaea peregra* in which range of sizes is much greater, a modified grouping into class intervals of 0·2 mm. was adopted before calculating. Separation of age-groups or "generations" within a sample was made in most cases on a basis of size (e.g. see the clear bimodality shown in Fig. 5 sample SQ12a). In a few cases this was checked by plotting the size distribution on probability paper as used by Harding (1949). To some extent in populations of *L. peregra* and much more clearly in stocks of *Planorbis albus* and *Valvata piscinalis*, older shells (e.g. those of snails which have overwintered) show a greater opacity of the periostracum. This distinction provided a clear verification of age-group separation by size in samples of *P. albus* and of *Valvata*. In one case only, a sample of *Valvata* was subdivided on the basis of shell opacity where no clear bimodality in size existed. In those cases where more than 100 individuals of a species had been collected in the sample, a random selection of 100 taken from it was measured. In all nearly 6,500

measurements were made on 4,868 snails. Of these, the results of measuring 54 samples (some subdivided, to include 73 subsamples), totalling 3,107 snails are presented here.

POPULATION DENSITY RELATIONSHIPS

Both total density of snails on the bank and relative numbers of the four species vary throughout the year. Nine standard dredge samples were taken at roughly seven-week intervals in 1952–53. Species-numbers are also shown as percentages of the total catch and, omitting the figures for *Valvata*, as percentages of the total pulmonate snails taken (both in brackets in Table 1). These numbers, resulting from dredge hauls, cannot provide any direct measure of the density of the snails. Some additional samples were taken with a small weighted Petersen grab (bite=approx. 370 sq. cm.) to assess actual densities. For example, at the same time as the dredge sample of 2/vi/53 (sample series number Q11), nine grab samples were taken, combined, then sieved and sorted like a standard dredge sample. The combined samples yielded fifty-three snails, corresponding to 159 per square metre. Thus the dredge sample (Q11—Table 1) of the same date, totalling 289 snails probably derived from 1·82 sq. m. of the bottom, or the haul covered a linear distance of about 3·6 m. Calculated in this way, different dredge hauls of the standard series are estimated to have covered between 1·5–4 sq. m. of the bottom, i.e. the hauls have swept linearly between 3 and 8 m. The latter figures are in accord with field estimates of the dredging. The fifty-two snails taken in the June grab samples were : fifteen *P. albus*, eight *Physa*, four *L. peregra*, and twenty-six *Valvata*, giving bottom densities of 45, 24, 12, and 78 per sq. m. respectively. The relative proportions of species from the grab samples are remarkably close to those from the standard dredge (Q11—Table 1). Population density figures for molluscs reported by Weerekoon (1956 a) from sampling done in 1949 are not dissimilar. It is unlikely that fluctuations from year to year in population densities of snails on this bank are ever as great as inshore where annual fluctuations in the adult population density at breeding can be five-fold in *L. peregra*, and three-fold in *Physa* (Hunter, 1961).

Changes in the relative numbers of the four species throughout the year are shown graphically as percentages in Fig. 2, and are extended into October 1953 by incorporating estimates from a small dredge sample (totalling only forty-eight snails) which was taken six weeks after the end of the main series, and not measured with the rest. The main fluctuations in numbers of each species correspond to the gradual dying-off of adults, and to increase following recruitment of a new generation of juveniles. This is close on the breeding season in *Planorbis*, *Physa* and *Lymnaea*, but not in *Valvata*. The three pulmonates average 0·57, 0·85, and 0·95 mm. at hatching and grow rapidly. Newly-hatched *Valvata* measure 0·3 mm. and grow only slowly to a size which is retained in the sieve used. It is mainly for this reason that the relative percentages of the three pulmonate species, disregarding *Valvata*, are set out separately in Table 1 and Fig. 2. The fluctuations in numbers of these three species can be considered in detail. Egg-masses of this population of *Planorbis albus* are found throughout, but mainly late in, July, with a few early

Table 1—Summary of standard samples of gastropods from an offshore bank in Loch Lomond, giving actual catch numbers and percentages of the four species in each sample.

Sample series nos.	Q1	Q3	Q4	Q6	Q7	Q9	Q11	Q13	Q16
Dates	14/ix/52	23/ix/52	16/xi/52	29/xii/52	13/ii/53	22/iv/53	2/vi/53	16/vii/53	31/viii/53
Total snail catch	286	316	359	319	382	460	289	310	358
Total pulmonates	201	227	315	288	306	292	136	169	324
Planorbis albus (b)	51	60	89	87	90	194	75	24	199
	(17·8)	(19·0)	(24·8)	(27·3)	(23·6)	(42·2)	(26·0)	(7·7)	(55·6)
	(25·4)	(26·4)	(28·3)	(30·2)	(29·4)	(66·4)	(55·1)	(14·2)	(61·4)
Physa fontinalis (a)	112	127	172	157	186	68	45	68	64
	(39·2)	(40·2)	(47·9)	(49·2)	(48·7)	(14·8)	(15·6)	(21·9)	(17·9)
	(55·7)	(55·9)	(54·6)	(54·5)	(60·8)	(23·3)	(33·1)	(40·2)	(19·8)
Lymnaea peregra (d)	38*	40	54	44	30	30	16	77	61
	(13·3)	(12·7)	(15·0)	(13·8)	(7·9)	(6·5)	(5·5)	(24·8)	(17·0)
	(18·9)	(17·6)	(17·1)	(15·3)	(9·8)	(10·3)	(11·8)	(45·6)	(18·8)
Valvata piscinalis (c)	85*	89	44	31	76	168	153	141	34
	(29·7)	(28·2)	(12·3)	(9·7)	(19·9)	(36·5)	(52·9)	(45·5)	(9·5)

In each entry, the upper figure is the actual number of the species from each sample. The figures in brackets below give these species-numbers : first as percentages of the total snail catch, and secondly, omitting the figures for *Valvata*, as percentages of the total pulmonate snails taken.

*These two sub-samples were not measured with the rest, and are omitted in subsequent tables.

in August. In the dredged samples a marked increase occurs between mid-July and the end of August, corresponding to the new generation. In *Physa*, egg-masses are found mostly at the end of May and in early June, decreasing in

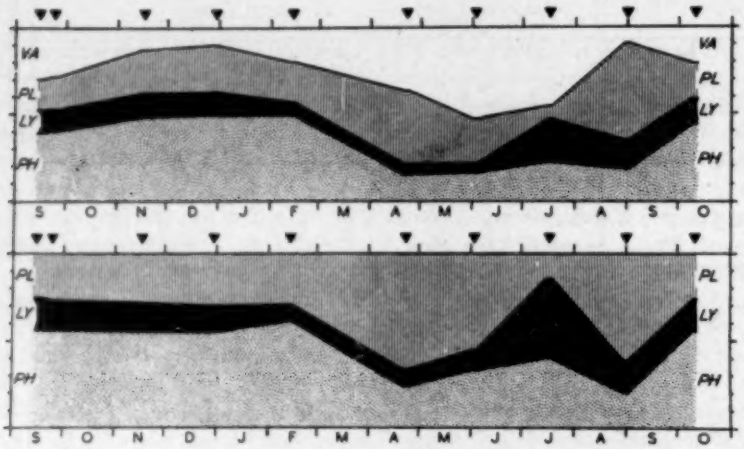

Fig. 2—The relative numbers of the four species in the standard dredge samples from the isolated offshore bank in Loch Lomond. Dates of samples are indicated by the black triangles, and the species-numbers shown as percentages in each dredge sample. (VA—*Valvata* ; PL—*Planorbis albus* ; LY—*Lymnaea peregra* ; and PH—*Physa*). The upper part shows the four species as percentages of the total snail catch, and the lower omits numbers of *Valvata* and shows percentages of the total pulmonate snails taken. For further explanation, see text.

late June and early July. The dredged samples show a proportionate increase in this species beginning before mid-July, but this is later swamped by the great increase in *P. albus* noted above. Lastly, in this population of *L. peregra*, infrequent egg-masses are found over a long period (from the end of March to early August), though the bulk of the season's eggs are found within three weeks at the end of May and the beginning of June. As shown in Fig. 2 (and Table 1), a marked increase in the proportion of this species in the dredged samples takes place before mid-July. These figures of proportionate densities are also relevant in assessing the death-rate of adults, but this will be discussed separately for each species after consideration of the size-data.

PLANORBIS ALBUS

Since they show the simplest growth pattern and life cycle, in many respects, the results for *Planorbis albus* are presented first. The maximum diameters of the shells were measured, and these are shown in the histograms of Fig. 3 which cover the year's standard samples from the offshore bank, and also two comparative samples. To allow comparison of the histograms, the frequency in each class is shown as a percentage of the total number in the sample. This is modified in the cases of the first two samples of the standard series (Q1b and Q3b), which were taken nine days apart. These are shown as

halves of a normal histogram. A summary of the size-data from these samples, including means and deviations, is given in Table 2. Certain samples were split, on grounds of shell opacity and size, into adults (suffix/A) and young (/Y). In Table 2, the smaller numbers of adults surviving after the breeding season are treated separately from the more numerous new generation in the samples from late August to mid-November (adults : Q16b/A, Q1b/A, Q3b/A and Q4b/A). In one case a single obviously early-hatched juvenile (Q13b/Y) is shown apart from the otherwise adult sample.

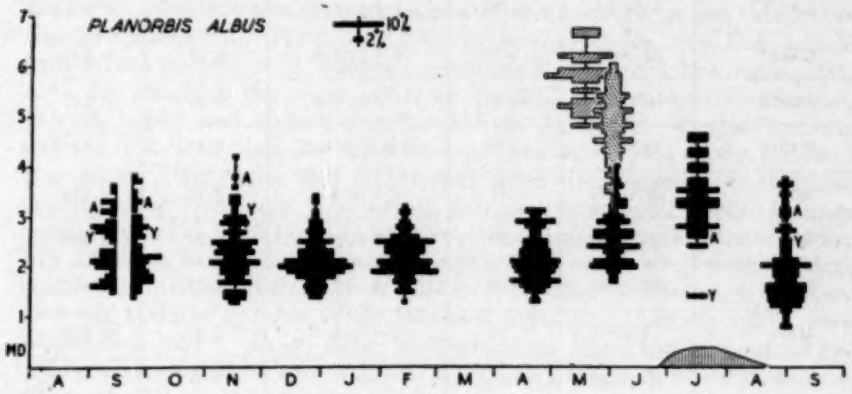

Fig. 3—Maximum diameters (MD) in millimetres of shells of *Planorbis albus*. The black histograms represent the standard dredge samples from the isolated offshore bank in Loch Lomond, and two comparative samples of breeding adults are shown : from an inshore locality in Loch Lomond (stippled), and from a relatively eutrophic pond (cross-hatched). Standard samples read : Q1b, Q3b, Q4b, Q6b, Q7b, Q9b, Q11b, Q13b, and Q16b from left to right. For further explanation, see text.

It should be emphasized that the limited populations of snails on McDougall Bank, which provide the standard samples, have poor feeding and grow slowly. Widespread collecting of *P. albus* from elsewhere in Scotland suggests that the average size is unusually low in this limited population. The breeding season of the standard population was noted earlier, and the occurrence of egg-masses is shown conventionally in Fig. 3—the greatest number being found in late July. The average development time from egg-laying to hatching in *Planorbis albus* at 14° to 18° C is fourteen days, and newly-hatched young from Loch Lomond egg-masses have a mean MD of 0·57 mm. In the laboratory, the newly-hatched snails if feeding on epiphytic diatoms can gain 0·45 mm. in the first twenty-one days after hatching, and this is probably less than the maximum initial growth which occurs in the field. Thus within about thirty-five days of laying, juvenile *P. albus* can be retained in the sieve used for the standard samples. Snails as small as 0·8 mm. have been sorted from a sample, though snails of 1·2 mm. are probably the smallest to be fully retained (e.g. see the form of the histogram Q16b/Y in Fig. 3). After the initial increase, there appears

Table 2—Summary of size data from standard samples of *Planorbis albus* in Loch Lomond (offshore bank), with two comparative samples.

Identification letters	Sample date	No. in sample	Range of diameters mm.	Mean diameter mm.	s.d. mm.
Q1b/Y	14/ix/52	41/51	1·5 to 2·9	2·2	0·444
Q1b/A	14/ix/52	10/51	3·0 to 3·6	3·25	0·191
Q3b/Y	23/ix/52	51/60	1·4 to 3·0	2·17	0·441
Q3b/A	23/ix/52	9/60	3·1 to 3·8	3·44	0·246
Q4b/Y	16/xi/52	86/89	1·3 to 3·4	2·27	0·527
Q4b/A	16/xi/52	3/89	3·6, 3·8, 4·2	3·87	—
Q6b	29/xii/52	87	1·4 to 3·4	2·14	0·416
Q7b	13/ii/53	90	1·3 to 3·2	2·22	0·396
Q9b	22/iv/53	100	1·3 to 3·1	2·17	0·475
Q11b	2/vi/53	75	1·7 to 4·0	2·71	0·589
Q13b/Y	16/vii/53	1/24	1·4	1·4	—
Q13b/A	16/vii/53	23/24	2·4 to 4·6	3·41	0·614
Q16b/Y	31/viii/53	86/100	0·8 to 2·8	1·75	0·48
Q16b/A	31/viii/53	14/100	2·9 to 3·7	3·31	0·266
AQ15	18/v/53	18	4·8 to 6·7	5·71	0·538
AQ17	2/vi/53	64	3·2 to 6·0	4·77	0·665

to be little or no growth in this species/population in the winter months. Growth begins again after April, and breeding size is reached by July. The histograms of Fig. 3 give a false impression of the rapidity of the dying-off of the adults after breeding. This is due to the enormous numbers of young recruited after August, exaggerating the decrease in adult numbers. Although the end of August sample shows only 14 per cent of surviving adults, if the catch percentages of Table 1 are employed, this represents a fall of only 40 per cent in their numbers from mid-July. About 6 per cent of adults can survive until November—perhaps a longer post-spawning survival than is usual in freshwater pulmonate snails. Survival is greatest around modal adult size, the range of size variability narrowing as adults die off after breeding. (This is shown in Table 2 by the marked decrease in the standard deviations of diameters in the adults surviving into the samples of late August and September).

Thus the life cycle of the standard limited population of *P. albus* runs as follows : hatching early August, growth till October, little growth November to April, then growth till breeding size reached in late July, some adults surviving after spawning until November (i.e. possibly to an age of sixteen months). In other populations of *P. albus* in the West of Scotland, no instance is known of more than one generation, or more than one breeding season, occurring in a year. Interpopulation differences in this species only concern rates of growth, adult size at breeding, and time of breeding season. The last two samples in Table 2 (AQ15 and AQ17) are typical of the many populations of *P. albus* in which adult size is greater, and breeding earlier, than in the standard population. The first, AQ15, is of breeding adults taken from a small hard-water eutrophic pond, Westerhouse Quarry Pool, Lanarkshire (see Hunter, 1955, for details of the other molluscan fauna). At the time of collection, 18/v/53, young were beginning to hatch from egg-masses—so that breeding had begun in late April, i.e. some three months before that of the standard population. The adults were 67 per cent larger than those of the standard population at breeding. The second comparative sample, AQ17, is from inshore waters of Loch Lomond, and consists of breeding adults from Boiden Lily Creek, a locally eutrophic/mesotrophic inlet south of Rossdhu. Egg-laying was intensive at the time of collection, 2/vi/53, i.e. breeding is some six to seven weeks in advance of the standard population, and the adults were 40 per cent larger. In *P. albus* (in Scotland at least) the interpopulation differences produced by better trophic conditions are simply increased growth rates and earlier breeding seasons.

PHYSA FONTINALIS

Considerable interpopulation differences, involving rates of growth as well as seasonal course of reproductive cycles, are found in *Physa fontinalis*. For the standard samples of this species from the offshore bank in Loch Lomond, the shell-lengths are shown in the histograms of Fig. 4. The frequency in each class is again shown as a percentage of the total number of the species in each sample, and the first two samples (Q1a and Q3a) are again shown as halves of a normal histogram. A summary of the size-data, including means and standard deviations, for these samples is given in Table 3. In only one case is a sample split : in mid-July, two surviving adults (Q13a/A) are treated separately from the more numerous new generation (Q13a/Y).

Here also poor feeding conditions on McDougall Bank determine that this limited population of *Physa* is relatively slow-growing with a simple annual life cycle. The seasonal occurrence of egg-masses is indicated in Fig. 4, the bulk of eggs being found at the end of May and in early June. At 13° to 18°C, the average time for the development of *Physa* from egg-laying to hatching is nineteen days, and egg-masses from Loch Lomond yield young of mean SL of 0·85 mm. Newly-hatched *Physa* can gain 1·1 mm. in the first twenty-one days after hatching in the laboratory, and the initial rate of growth in the natural population is probably greater. All snails of SL > 1·2 mm. are retained by the sampling method, and the new generation has a mean SL of 1·95 mm. by mid-July (the maximum SL being 3·4 mm.). The rapid initial growth appears

to continue until late October, with little growth from November to February. Growth resumes about March, and breeding size is reached in May. Thus the winter period of little or no growth is at least two months shorter than that for *Planorbis albus* living in the same habitat. Again, the histograms of Fig. 4

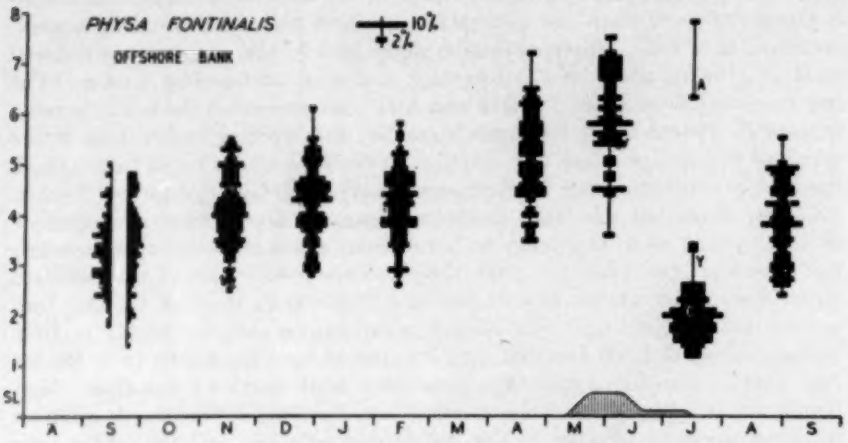

Fig. 4—Shell lengths (SL) in millimetres of *Physa fontinalis* in the standard dredge samples from the isolated offshore bank in Loch Lomond. Standard samples read : Q1a, Q3a, Q4a, Q6a, Q7a, Q9a, Q11a, Q13a, and Q16a from left to right. For further explanation, see text.

Table 3—Summary of size data from standard samples of *Physa fontinalis* in Loch Lomond (offshore bank).

Identification letters	Sample date	No. in sample	Range of lengths mm.	Mean length mm.	s.d. mm.
Q1a	14/ix/52	100	1·8 to 5·0	3·27	0·678
Q3a	23/ix/52	100	1·4 to 4·8	3·46	0·798
Q4a	16/xi/52	100	2·5 to 5·5	4·09	0·699
Q6a	29/xii/52	100	2·8 to 6·1	4·23	0·7
Q7a	13/ii/53	100	2·6 to 5·8	4·18	0·67
Q9a	22/iv/53	68	3·5 to 7·2	5·15	0·837
Q11a	2/vi/53	45	3·6 to 7·5	5·91	0·892
Q13a/Y	16/vii/53	66/68	1·2 to 3·4	1·95	0·44
Q13a/A	16/vii/53	2/68	6·3 and 7·8	7·05	—
Q16a	31/viii/53	64	2·4 to 5·5	3·82	0·758

somewhat exaggerate the decrease in adult numbers after spawning: the adults surviving in mid-July (Q13a/A) make up only 3 per cent of the sample, but are equivalent to about 6·5 per cent of the adult population at the previous sample. Probably all adults would be dead by September, i.e. few reach the age of fourteen months. In this population of *Physa* survival of adults after spawning is less than in *Planorbis albus*, but, in other respects, the simple life cycle is similar.

The main comparative data on *Physa* are drawn from an inshore littoral population in Loch Lomond. The shell lengths of samples are shown in the histograms of Fig. 5, the class frequencies again being shown as percentages of each sample number. The data are summarized, with means and standard

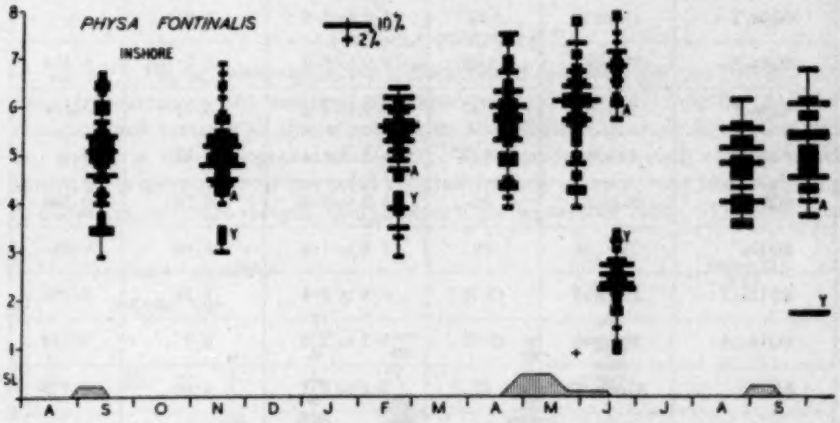

Fig. 5—Shell lengths (SL) in millimetres of *Physa fontinalis* in comparative samples from an inshore littoral population in Loch Lomond. Comparative samples read: SQ2a, SQ5a, SQ8a, SQ9a, SQ10a, SQ12a, SQ15a, and SQ17a from left to right. For further explanation, see text.

deviations, in Table 4. The life cycle of this population is obviously more complex. Egg-masses were found not only in the main breeding season from late April to late May—with a few eggs until mid-June—but also in small numbers during the first half of September. There is apparently no consequent replacement of one generation by another, and snails born in early summer make up the bulk of the over-wintering stock. In analysis, several samples have been split (see Table 4): in the samples of late autumn and winter (SQ17a, SQ5a, SQ8a) the autumn-born snails are treated separately, and in the late June sample (SQ12a) the surviving adults are separated from the new generation. It should be noted here that at the end of May (SQ10a, 29/v/53) some newly-hatched young were present though not taken in the sample. Some of the snails hatched in early summer have grown and matured so rapidly as to be able to breed themselves before the autumnal fall in temperature. At the time of the autumn spawning, although the mean SL of the generation born around the end of May was only 4·98 mm. (in 1952—by interpolation in Table 4,

similar in 1953), the maximum SL of the stock was 6·7 mm. It is almost certain that the relatively few mature snails in the stock were exclusively those in the size group, 5·8 to 6·7 mm. From the Loch Lomond data, there is no was of deciding whether the individual snails which spawn in autumn then die, or whether they survive to spawn again in the late spring of the next year.

Table 4—Summary of size data from inshore comparative samples of *Physa fontinalis* in Loch Lomond.

Identification letters	Sample date	No. in sample	Range of lengths mm.	Mean length mm.	s.d. mm.
SQ2a	12/ix/52	63	2·9 to 6·7	4·98	0·936
SQ5a/Y	17/xi/52	6/64	3·0 to 3·5	3·23	—
SQ5a/A	17/xi/52	58/64	4·0 to 6·9	5·1	0·628
SQ8a/Y	22/ii/53	10/47	2·9 to 4·2	3·71	0·404
SQ8a/A	22/ii/53	37/47	4·5 to 6·4	5·53	0·51
SQ9a	22/iv/53	52	3·9 to 7·5	5·73	0·896
SQ10a	29/v/53	50	3·9 to 7·8	5·86	0·93
SQ12a/Y	20/vi/53	47/73	0·9 to 3·4	2·34	0·558
SQ12a/A	20/vi/53	26/73	5·7 to 7·9	6·7	0·582
SQ15a	27/viii/53	22	3·5 to 6·1	4·68	0·713
SQ17a/Y	2/x/53	2/24	1·7	1·7	—
SQ17a/A	2/x/53	22/24	3·7 to 6·7	5·09	0·762

The snails which hatch from the eggs laid in this subsidiary breeding period in early September make only a small part of the overwintering stock. In growth samples taken during the winter the small number of autumn-born *Physa* can be distinguished on a basis of shell length, but from March onwards such separation is impossible. The spring growth of the younger snails has allowed them to "catch up" with the majority. It is possible that the February sample (SQ8a) shown is subdivided wrongly, so that apparently a larger proportion of the younger group has survived. This late egg-laying is known to have occurred in 1952, 1953, 1955, 1956, 1958 and 1959. There is no evidence that the incidence or extent of this subsidiary breeding season is in any way connected with summer water temperatures, or with any other obvious variable in the weather. The number of young hatching and surviving is usually small, and it seems that the autumn-hatched snails rarely make up more than 8 per cent of the overwintering stock. For example, in a sample taken on 27/ix/59, after a very warm summer, the average density of this littoral population of

Physa was fifty-six per sq. m., but newly-hatched young were patchy in distribution and made up only 4·5 per cent of the population.

To recapitulate, in the limited population of *Physa fontinalis* on the offshore bank, there is a simple annual life cycle, the snails growing for one year and dying after spawning in a single breeding season. Secondly, in the inshore population of *Physa* there can be two generations in a year, but no replacement of one generation by the other. Thirdly, a detailed study by De Wit (1955) of a population of *Physa fontinalis* at Botshol, Utrecht, Holland, has shown that there two generations per year occurred, with complete replacement of the spring-born, by an overwintering, generation. Thus in this species, infraspecific variation, corresponding to different trophic and climatic conditions, involves the course of the reproductive cycle, as well as growth rates.

LYMNAEA PEREGRA

As with *Physa*, interpopulation differences in *Lymnaea peregra* involve not only growth rates but seasonal reproductive cycles. Shell-lengths (SL) for the standard samples of this species from the offshore bank in Loch Lomond are shown in the histograms of Fig. 6. The frequency in each class is again shown as a percentage of the total number in each sample. At the beginning of the series, only one sample (Q3d) is shown for September 1952. The size-data

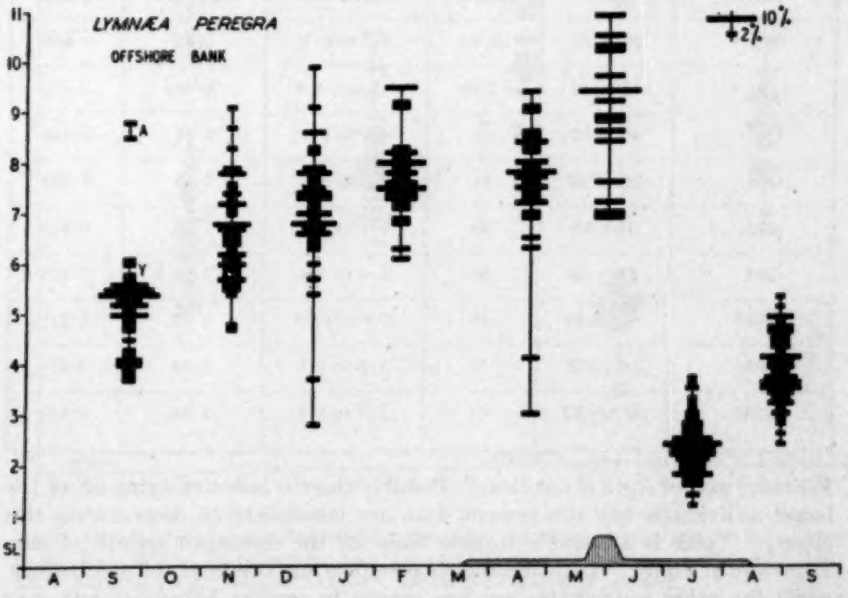

Fig. 6—Shell lengths (SL) in millimetres of *Lymnaea peregra* in the standard dredge samples from the isolated offshore bank in Loch Lomond. Standard samples read : Q3d, Q4d, Q6d, Q7d, Q9d, Q11d, Q13d, and Q16d from left to right. For further explanatiion, see text.

are summarized in Table 5. The only sample split is the first (Q3d), in which two surviving adults (one year plus) are treated separately from the numerous young snails born earlier that summer. Again the limited population living on McDougall Bank has markedly lower average size than other stocks. As with *Planorbis albus* and *Physa fontinalis*, the limited stock shows a simple annual life cycle—though in *L. peregra* growth apparently continues through the winter months. The reproductive period in this species/population is less clearly defined : egg-masses are found from late March to early August, though for most of this long period they are very rare. The great bulk of the year's eggs are found within three weeks at the end of May and the beginning of June. This is shown conventionally in Fig. 6. The newly-hatched young have a mean SL of 0·95 mm. and, in the laboratory, can reach an SL of 2·1 mm. twenty-one days after hatching. All spat of SL>1·2 mm. are retained by the sampling method and the main part of the new generation is recruited to the samples by mid-July (see histogram in Fig. 6). In this species/population steady growth appears to continue from July till February at least. The significance of the fall in mean size of the population between the samples of

Table 5—Summary of size data from standard samples of *Lymnaea peregra* in Loch Lomond (offshore bank).

Identification letters	Sample date	No. in sample	Range of lengths mm.	Mean length mm.	s.d. mm.
Q3d/Y	23/ix/52	38/40	3·7 to 6·1	5·02	0·658
Q3d/A	23/ix/52	2/40	8·5 and 8·8	8·65	—
Q4d	16/xi/52	54	4·7 to 9·1	6·61	0·933
Q6d	29/xii/52	44	2·8 to 9·9	7·08	1·202
Q7d	13/ii/53	30	6·1 to 9·5	7·76	0·813
Q9d	22/iv/53	30	3·0 to 9·4	7·54	1·306
Q11d	2/vi/53	16	6·9 to 10·9	8·93	1·271
Q13d	16/vii/53	77	1·2 to 3·7	2·32	0·521
Q16d	31/viii/53	61	2·4 to 5·3	3·88	0·648

February and of April is not clear. Possibly there is selective dying-off of the larger individuals but the present data are insufficient to demonstrate this clearly. There is a possible trophic basis for the continued growth of only *L. peregra* in winter. In its feeding, *L. peregra* is unspecialized and omnivorous, while the other pulmonates are less plastic in feeding behaviour and may require living green plants for continued growth. Such biological differences between *Lymnaea*, *Ancylus* and *Physa* are discussed elsewhere (Hunter, 1961). The mean size of the population at the time of maximum reproductive activity

must be about 8·5 mm. SL. The samples offer little direct evidence on the survival of adults after breeding. Although the late September sample (Q3d) would indicate 5 per cent of the population as surviving (fifteen month old) adults, this is unusual. Most adults must die very soon after spawning.

Some data have been collected from inshore populations of *L. peregra* within Loch Lomond, but these are not used because of certain complexities. Two distinct types of egg-masses of this species are found in these habitats. There is some other evidence that the inshore populations of *L. peregra* are mixed stocks of two physiological races having different reproductive rates and probably different growth-rate patterns. A simpler contrast is provided by a population of *L. peregra* living in a tributary river of Loch Lomond, the Fruin Water, in a large pool about 1·8 miles (3 km.) from the loch. The main comparative data are drawn from this population and the shell lengths of samples are shown in the histograms of Fig. 7. As before, class frequencies are shown as percentages of the total number in each sample, and the data are summarized, with means and standard deviations, in the first part of Table 6. This is a less extensive population than the others discussed, and sampling was

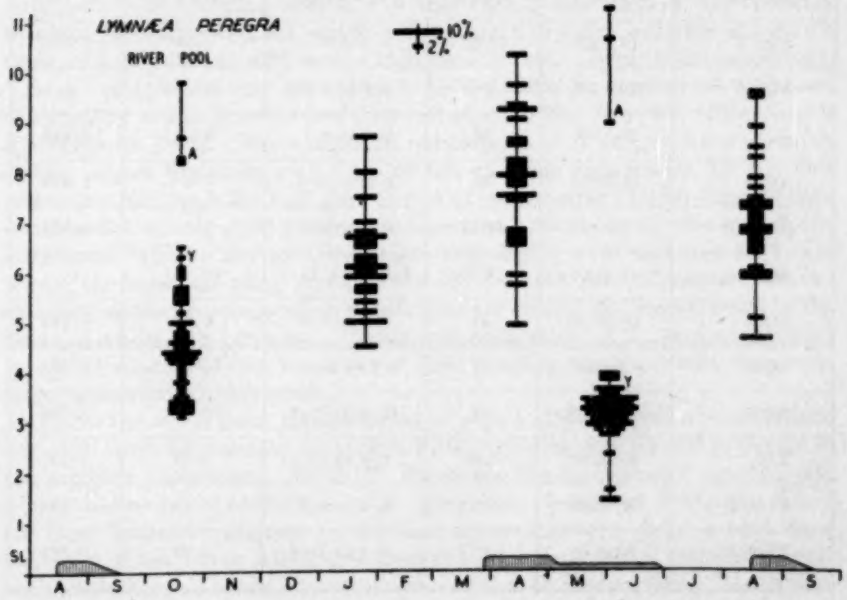

Fig. 7—Shell lengths (SL) in millimetres of *Lymnaea peregra* in comparative samples from a pool in the Fruin Water, 1·8 miles from Loch Lomond. Comparative samples read : AQ5, AQ8, AQ14, AQ19, and AQ22 from left to right. For further explanation, see text.

deliberately less. The life cycle in this species/population clearly involves two generations per year with complete replacement. This pattern of life cycle is not uncommon in other populations of *L. peregra* living in smaller

eutrophic lakes and in certain rivers in the West of Scotland. Two samples are split for analysis (AQ5 and AQ19—see Table 6 and Fig. 7), and in both the few surviving adults of the earlier generation are clearly distinguished on a size basis. The overwintered adults are larger than the spring-born generation, at their respective periods of reproduction. Many egg-masses are found throughout April, a few also in May and June. Egg-masses are again common in the second half of August, with fewer in early September. In both May and September, the newly hatched snails have an initial high growth rate, which is sustained in the summer generation. The data suggest that in the overwintering generation growth is slowed in December and January, unlike the condition in the offshore population of *L. peregra* in Loch Lomond. However, growth rates higher than those in the standard population are possible throughout most of the year, and the life cycle involves two generations.

Table 6—Summary of size data from comparative samples of *Lymnaea peregra* in Fruin Water, near Loch Lomond, with other comparative samples.

Identification letters	Sample date	No. in sample	Range of lengths mm.	Mean length mm.	s.d. mm.
AQ5/Y	19/x/52	58/62	3·1 to 6·5	4·49	0·891
AQ5/A	19/x/52	4/62	8·2 to 9·8	8·75	—
AQ8	25/i/53	23	4·5 to 8·7	6·23	0·981
AQ14	14/iv/53	25	4·9 to 10·3	7·8	1·308
AQ19/Y	2/vi/53	49/52	1·4 to 3·9	3·1	0·533
AQ19/A	2/vi/53	3/52	8·9, 10·6, 11·2	10·23	—
AQ22	18/viii/53	31	4·6 to 9·5	6·89	1·198
AQ46	2/vi/56	51	8·8 to 15·2	11·48	1·725
AQ50	23/vii/56	19	12·8 to 17·4	15·11	1·755
T177	30/ix/58	36	6·8 to 14·1	9·22	1·332
T178/Y	30/ix/58	21/72	4·2 to 6·2	5·34	0·534
T178/A	30/ix/58	51/72	6·8 to 10·6	8·08	0·865

Further examples of interpopulation differences in *L. peregra* are illustrated by the four samples for which data are summarized in the second part of Table 6. The first of these (AQ46) is a sample of breeding adults from a highland but mesotrophic stream, at 365 feet above sea level, where *Ancylus* is regularly sampled, the Upper Craigton Burn, near Glasgow. The main breeding season here covers about three weeks in May. A small number of eggs is laid in the first half of September by some of the May-hatched snails.

Thus the pattern of life cycle in this stream population of *L. peregra* is similar to that of *Physa fontinalis* in inshore populations in Loch Lomond, though in the Upper Craigton Burn the proportion of survivors of this second brood in the overwintering stock varies greatly from year to year. The breeding adults in May are much larger than adult *L. peregra* of the Fruin population, in which two full generations per year occur. This implies that the rate of maturing is not simply linked to rate of growth. Although in spring the water of the Upper Craigton Burn is cooler than that of the Fruin Water, this factor in itself seems insufficient to account for the difference in reproductive cycles. Possibly there is a genotypic difference between these populations in size at, and time of, breeding.

The next sample (AQ50) is from a highland stream in limestone country just above sea level near Eriboll on the east side of Loch Eirebol on the north coast of Scotland. Although the population was sampled in late July the snails were copulating and egg-laying, no juveniles were present, and it seemed that the breeding season was just beginning. These adults were relatively large (mean SL=15·11 mm., see Table 6), so that neither insufficient size for spring maturity, nor low water temperatures, could be responsible for the lateness of the breeding season. In this case genetic factors are certainly involved in determining mid-summer breeding, and hence a simple annual life cycle, in a population with such a high growth rate. Bred in the laboratory, " races " of *Lymnaea* spp. are known to show genetically determined variations in fecundity and in growth rates (Boycott *et al.*, 1930 ; Boycott, 1936 ; Forbes & Crampton, 1942). Many highland populations of *L. peregra* have a similar simple annual life cycle with mid- or late-summer replacement by the new generation, although the high growth rate of the example (AQ50)—due to hard water and relatively good trophic conditions at Eriboll—is not common in the Highlands. [These last samples (AQ45 and AQ50) were taken in 1956, not during the main sampling period (1952–53), but the size differences from the standard and main comparative populations are clearly significant, being of the order of 40 to 130 per cent. Within one population of *L. peregra* sampled yearly (Hunter, 1961) the mean size of 1956 breeding stock was only 8 per cent larger than that of 1953 stock.]

Given the above data, measurement of even a single sample of known date can yield some information on growth rates, breeding seasons and life cycle in the sampled population. Mr A. E. Henderson kindly collected two samples from " unknown " populations of *L. peregra* in Northwest Scotland. They are from limestone country in the Lochcarron district : from a pool on a tributary of the River Kishorn, a quarter of a mile south of Couldoran, and from the hill source of the stream whose outfall is at Portnacrich. The former pool lies about 40 feet about sea-level, and the latter at about 890 feet : they are here referred to as the " lower pool " and " higher pool " samples. Both were taken at the end of September. The higher pool sample (T177, see Table 6) appears to cover only one generation, while the lower pool (T178/A and T178/Y) shows a bimodal size distribution. Snails of less than 3 mm. SL could have been present in the higher pool and not collected. In both a single generation per year is postulated, with the late replacement characteristic of many

poorer highland localities, although the snails in these populations, due to harder water, are larger and of slightly " higher spired " form than most in the Highlands. The population in the lower pool must begin to breed earlier (by about four to five weeks) than that in the higher pool. The adults do not die soon after breeding as in most stocks—but the larger individuals of the lower pool die off more rapidly, so that larger adults will be found later in the year in the higher pool.

Thus, in *Lymnaea peregra* as in *Physa fontinalis*, infra-specific differences between populations involve the seasonal course of life cycles as well as growth rates, and it seems likely that certain of the interpopulation differences are not merely environmentally derived, but are genetically determined.

VALVATA PISCINALIS

The fourth species in the standard samples is the only prosobranch : the " aspidobranch " mesogastropod, *Valvata piscinalis*. Unlike most prosobranchs, it is hermaphrodite, with a diaulic genital system structurally reminiscent of the pulmonates, and a life cycle not greatly dissimilar in functional aspects of growth and reproduction. In the standard samples of *V. piscinalis*, the maximum diameters (MD) of the shells were measured and these are shown in the histograms of Fig. 8, along with one comparative sample

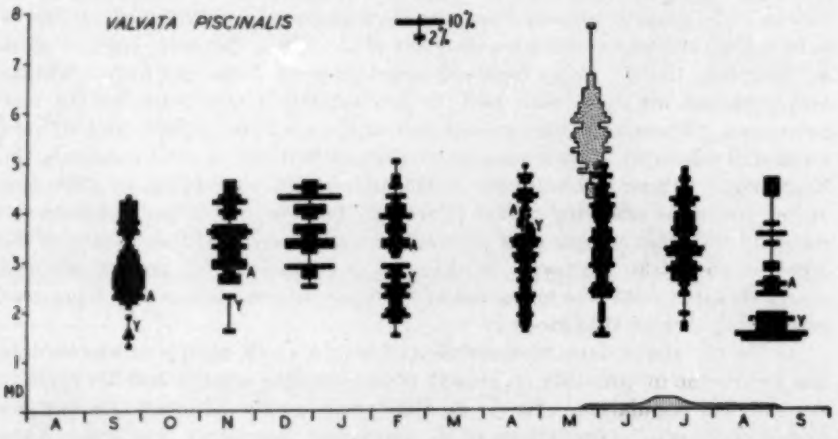

Fig. 8—Maximum diameters (MD) in millimetres of shells of *Valvata piscinalis*. The black histograms represent the standard dredge samples from the isolated offshore bank in Loch Lomond, and one comparative sample of breeding adults is shown (stippled) from a relatively eutrophic lowland loch—Castle Loch, Lochmaben, Dumfriesshire. Standard samples read : Q3c, Q4c, Q6c, Q7c, Q9c, Q11c, Q13c, and Q16c from left to right. For further explanation, see text.

from a population in a more eutrophic habitat. The frequency in each class is shown as a percentage of the total number in each sample. Only one sample (Q3c) is shown for September 1952—at the beginning of the series. A summary of the size-data for *V. piscinalis* is given in Table 7, including means and

deviations. In three autumn samples (Q3c, Q4c and Q16c), obvious juveniles are treated separately. Further, in two winter samples (Q7c and Q9c) two

Table 7—Summary of size data from standard samples of *Valvata piscinalis* in Loch Lomond (offshore bank), with one comparative sample.

Identification letters	Sample date	No. in sample	Range of diameters mm.	Mean diameter mm.	s.d. mm.
Q3c/Y	23/ix/52	5/89	1·3 to 1·9	1·56	—
Q3c/A	23/ix/52	84/89	2·1 to 4·3	3·06	0·621
Q4c/Y	16/xi/52	2/44	1·6 and 2·3	1·95	—
Q4c/A	16/xi/52	42/44	2·6 to 4·6	3·5	0·559
Q6c	29/xii/52	31	2·5 to 4·6	3·66	0·598
Q7c/Y	13/ii/53	35/76	1·5 to 2·9	2·33	0·376
Q7c/A	13/ii/53	41/76	3·1 to 5·0	3·83	0·457
Q9c/Y	22/iv/53	71/100	1·6 to 3·9	2·86	0·631
Q9c/A	22/iv/53	29/100	3·6 to 4·9	4·19	0·358
Q11c	2/vi/53	100	1·5 to 4·9	3·36	0·86
Q13c	16/vii/53	100	1·6 to 4·8	3·36	0·699
Q16c/Y	31/viii/53	18/34	1·4 to 1·9	1·61	0·176
Q16c/A	31/viii/53	16/34	2·3 to 4·6	3·26	0·838
AQ18	27/v/53	61	4·3 to 7·7	5·6	0·607

generations of snails (ca. eight and ca. twenty months old) were present. In the February sample (Q7c), separation on a basis of shell opacity was confirmed by bimodality of sizes ; in the April sample (Q9c), separation depends on shell condition alone since there is a small overlap in the two size ranges (see histogram in Fig. 8, and Table 7). Growth is slow and, in *Valvata* as in the other species, the limited population of the offshore bank is of low average size.

The reproductive season is long in the offshore population, eggs being found from late May until early September, with more in early July (see Fig. 8). Development from the formation of the spherical egg-capsule to hatching takes about seventeen days (the development period seeming to vary more than with pulmonate eggs), and the newly-hatched spat average 0·3 mm. MD, i.e. much smaller than most pulmonate spat. In the laboratory a size of 0·6 mm. MD can be reached twenty-one days after hatching. There is little evidence on the initial growth rate in the field. In this respect the standard samples are of less value for *V. piscinalis* than for the other three pulmonate species. It

seems likely that, with the shell shape of *Valvata*, snails of 1·4 mm. MD are the smallest likely to be retained. The occurrence of young snails in the dredge samples may be affected by seasonal change of habits. Cleland (1954), describing populations of *V. piscinalis* in the River Colne, Middlesex, noted that the adults in spring and summer lived on aquatic plants or on the surface of the mud, while the young in autumn and winter burrowed in the mud. The most important vegetation where the standard samples were collected in Loch Lomond is *Nitella opaca*, which dies down over winter. Although the halfway point of hatching in this population must come about mid-July, young snails hatched in 1952 do not appear in the samples to any extent, until February 1953 (i.e. aged ca. seven months). The first hatched young snails of 1953 have grown more rapidly since they appear in a sample at the end of August 1953 (i.e. aged two to three months). Growth appears to continue through the winter, and breeding size has been reached by some snails in late May. (In the laboratory, egg-capsules have been produced by *Valvata* of 3·2 to 5 mm. MD). The adult snails die off after spawning but death is not so immediate as in the pulmonates. The catch numbers of Table 1 used with the data of Table 7, suggest that at the end of December about 14 per cent of the adults which spawned during the previous summer are living, and in the following April about 9 per cent are still alive (aged probably twenty to twenty-one months), though none survive their second spring. In considering survival in *Valvata* some conclusions can be drawn from the occurrence of dead shells in the samples. Unlike the shells of the pulmonate species in the "soft" waters of Loch Lomond, the *Valvata* shells do not break down immediately after the death of the snail but persist for some weeks, as do the opercula (Hunter, 1954). Dead shells are found in the standard samples from September to April, being most numerous in autumn and spring, and they are almost all in the size groups 3·8 to 5 mm. MD.

In summary, the life cycle of *Valvata* in the standard limited population runs as follows: hatching within the period June to early September, slow growth throughout the year, breeding when a year old, growth continuing after breeding, adults reaching varying ages from thirteen to twenty-one months. All other populations known are also annual but with better feeding conditions the snails grow faster, adults die younger, and the breeding season is earlier and more intensive. In the River Colne population described by Cleland (1954) the growth rate was little higher than in Loch Lomond, but reproduction began in late April and reached a peak in June (though some egg-laying occurred in July), and most of the adults died off in August (aged thirteen to fifteen months). The comparative sample of *Valvata piscinalis* presented here (AQ18 in Table 7) was dredged from a relatively eutrophic lowland loch—Castle Loch, Lochmaben, Dumfriesshire, at the end of May. Egg-capsules were about five times more numerous than snails, indicating that the breeding season is more intensive (and thus likely to be shorter) than in Loch Lomond. The adults were at least 40 per cent larger than breeding adults in Loch Lomond, no small immature snails were present such as occur in early summer in Loch Lomond, and dead adult shells were taken in the sample. Another result of the higher rate of growth is that this Lochmaben population of *Valvata* has

relatively high-spired, more turbinate shells than the Loch Lomond stock. In general, populations of *Valvata piscinalis* in highland lochs in Scotland have small shells with the characteristics of shell form associated with low growth rates : relatively low spire and large open umbilicus. Specimens dredged from Loch Lubnaig by Annandale (1924) showed the latter characteristic and corresponded closely with examples from continental Europe of *Valvata alpestris* (Blauner). Annandale considered them to be a " phase " of *V. piscinalis* and assigned this highland shell form to *Valvata piscinalis* var. *alpestris* (Blauner). To recapitulate, all known populations of *Valvata piscinalis* are annual, with only one breeding season in each year. Populations under better trophic conditions show increased growth rates ; the breeding season earlier, more limited in time, and more intensive ; and adult survival less.

ANCYLUS FLUVIATILIS

No new data are presented on the pulmonate limpet, *Ancylus fluviatilis* which, apart from the four species already discussed, is the only freshwater snail abundant in the West of Scotland. The earlier paper on the growth and life cycle of *Ancylus* (Hunter, 1953 a) was mainly concerned with the population in a typical highland stream locality. In the Upper Craigton Burn, near Glasgow, *Ancylus* has a simple annual life cycle. The majority of limpets grow for one year and die soon after spawning. Egg-laying takes place from late April to mid-June in the Craigton Burn, and the young limpets which hatch after about twenty-five days, have a high initial growth rate. Growth continues relatively rapidly (ca. 0·22 mm. AL per ten days) to the end of October when some of the limpets are approaching " adult " size, then slows down (ca. 0·09 mm. AL per ten days) until March, when a short period at a higher growth rate accompanies the beginning of reproduction. The size of breeding adults varies, both from locality to locality and from year to year in the same place, and it was suggested that there is some environmental limitation of growth in *Ancylus* in normal habitats, i.e. in highland streams. The growth data from the typical stream population (Hunter, 1953 a) provide the basis of the *Ancylus* part of the life cycle diagram in the present paper (Fig. 9A). Geldiay (1956) compared different local populations of *Ancylus* in various habitats in the English Lake District. In the most typical habitat for these limpets, the " becks " of the district, he found the same pattern of growth and life cycle as in the " burns " of the West of Scotland. In certain habitats with lower overall growth rates the breeding season was two to three months later. Thus, there has to be considerable growth in spring and early summer before reproduction begins. In Windermere, both patterns of growth are found in different habitats on stony inshore bottoms. In one instance, Geldiay had evidence of breeding recurring in late summer. This " second generation " was of the type described above for the inshore populations of *Physa* in Loch Lomond, and made up only a small part of the overwintering stock, there being no " replacement ". Finally, in a lochan at an altitude of 1450 feet on the Isle of Skye, Scotland, the breeding season of *Ancylus* appears to be about nine weeks later than at sea-level, and the breeding limpets about 26 per cent smaller (Hunter & Hunter, 1956). Thus, in *Ancylus fluviatilis*, interpopulation

differences involving rates of growth and times of breeding are found, but almost all populations of this limpet show a simple annual life cycle.

COMPARATIVE DISCUSSION OF LIFE CYCLES

An earlier paper (Hunter, 1953 a) on growth and life cycle in *Ancylus* referred to the erroneous assumption by certain authorities (Cooke, 1895 ; Pelseneer, 1906 ; Baker, 1911) that a biennial life cycle is general in freshwater pulmonates. Recently a number of field studies have been reported including those of Cleland (1954), De Wit (1955—Holland), De Witt (1955—U.S.A.), Geldiay (1956), Duncan (1959), and Hunter (1957, 1961). With the exception of De Wit's study, mentioned above (p. 149), of a population of *Physa fontinalis* in which two generations per year occurred, these recent studies indicate that a simple annual life cycle is usual in freshwater snails. In a population with such a life cycle, the majority of individual snails grow for one year and die after spawning, and there is usually a single clear-cut breeding season in late spring or early summer. However, in different populations of each species, it is now clear that the simple cycle can vary markedly in growth rates and in the seasonal course of the reproductive cycle. Data on the extent of such interpopulation differences in five species have been presented here. Although these data were mostly drawn from the West of Scotland, comparable interpopulation, infraspecific variations occur almost certainly in freshwater snail populations throughout temperate latitudes.

Available evidence on freshwater prosobranchs is slighter. In *Valvata piscinalis*, all known populations are annual with only one breeding season. Populations in poorer trophic conditions (including " highland " lochs) show lower growth rates, a summer breeding season which is long and not intensive, and considerable adult survival with growth after breeding. Better conditions produce the converse. Size variation is comparable to that found in pulmonates, although *V. piscinalis* grows more slowly and possibly more continuously. It is likely that *Valvata cristata*, at least in populations in Scotland, has a similar life cycle. The hermaphrodite species of *Valvata* are most likely to resemble the freshwater pulmonates. Other common prosobranchs in Britain, such as *Bithynia* spp. and *Viviparus* spp. have separate sexes, and *Potamopyrgus jenkinsi* is parthenogenetic and ovo-viviparous. Some populations of *Bithynia tentaculata* breed after one year (Lilly, 1953), but in others, snails live for more than two years (Schäffer, 1953). *Viviparus* can live for several years, and several species show sexual dimorphism, the males being smaller. Judging by its growth rates, *Potamopyrgus* could get through two or three generations in a year, and young are found at all times. *Valvata*, *Bithynia*, *Viviparus* and *Potamopyrgus* all can feed, and presumably grow, during the winter months.

Data on interpopulation variations in growth and fecundity in freshwater pulmonates are more extensive. A series of characteristic life cycles is summarized in Figs. 9A & B, a version of which, though then unpublished, was used and discussed at the Glasgow meeting of the British Association in 1958 (see reports in Yonge, 1958 ; Haslett, 1958). Smoothed curves show seasonal changes of mean shell size in natural populations of snails, and the onset of

egg-laying and presence of developing egg-masses are indicated. Each horizontal axis is divided in months, and the solstices and equinoxes marked, and both potential sunlight and actual sunshine shown graphically. These last figures of hours of actual " bright sunshine " are average figures for ten years prepared from records kept by the Parks Department of the Corporation of Glasgow for Springburn Park in the north of Glasgow, but are broadly applicable to all the stations where snails were sampled in the West of Scotland. (The writer's thanks are again due to Mr G. H. Garside, Director of Parks, Glasgow.)

Considering these life cycles in broad outline (Figs. 9A & B), examples **1**, **2**, **3**, and **6** are of simple annual life cycles (i.e. those of *Planorbis albus*, *Physa* and *Lymnaea peregra* in the poor feeding conditions of the offshore bank in Loch Lomond, and that of *Ancylus* in a highland stream). Within these and similar simple annual cycles, two main patterns of growth and reproduction can be distinguished. There can be considerable growth of snails in the spring and early summer before a, relatively late, summer reproductive period (e.g. example **2** of *Planorbis albus*). In the other pattern, the stock of snails has grown before winter to nearly adult size and the breeding season then takes place in spring, after little post-winter growth (e.g. example **6** of *Lymnaea peregra* from the offshore bank). The onset of the reproductive season is determined differently in these two patterns : in the first by causes endogenous to the snails, in the second by environmental factors (both discussed below). But. in several species of freshwater pulmonates both patterns, " late-breeding " and " spring breeding ", occur in different populations. In *Planorbis albus*, the population offshore in Loch Lomond shows a late-breeding pattern, while other populations inshore in Loch Lomond and in a small eutrophic pond show the spring breeding pattern (see § 4 of this paper, Table 3 and Fig. 3). In *Ancylus fluviatilis*, spring breeding was found in the most typical populations—those of highland streams—by Hunter (1953 a) in the West of Scotland, and Geldiay (1956) in the Lake District. Geldiay also found populations with the late-breeding pattern in streams, and both patterns in Windermere itself in different habitats. Hunter and Hunter (1956) also noted late-breeding of *Ancylus* in a mountain lochan. For *Lymnaea peregra*, examples of both spring breeding populations, and of late-breeding involving considerable growth in spring and early summer, have been found, and examples are given in § 6 of this paper. In most known annual snail populations, the simple cycle could be classed in one or other of the two patterns, late-breeding or spring breeding, and surprisingly few life cycles are intermediate in character.

Leaving simple annual life cycles, example **4** in Fig. 9A, *Physa* from inshore in Loch Lomond, can next be considered. In this population, there is a small amount of breeding activity in the late summer. Thus there can be two generations in a year, but no replacement of one generation by the other. Some of the snails hatched in early summer have matured so rapidly as to be able to breed before the autumnal fall in water temperatures. The progeny of these snails are only a small fraction of the overwintering stock of *Physa* in this population (see § 5 of this paper). A similar pattern of life cycle is shown by a population of *Lymnaea peregra* in a mesotrophic highland stream (see § 6

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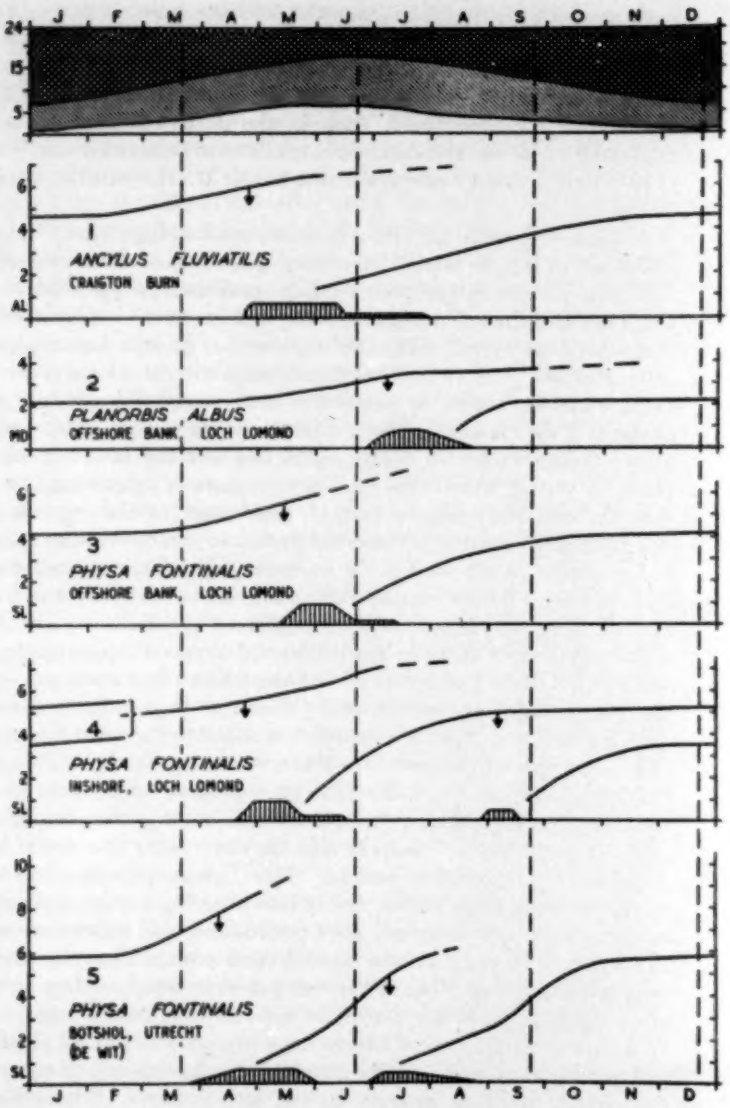

Fig. 9A.

Figs. 9A and 9B—Natural life cycles of populations of freshwater pulmonate snails: showing the presence of developing egg-masses. Months are indicated on each horizontal axis, broken At the top of each series are shown, in hours per day throughout the year, the potential period of figures for the Glasgow area in the years 1948–57. The mean size curves are smoothed, and based on data in this paper, 1 on data from Hunter (1953 a), 5 from De Wit (1955), 8 from Walton

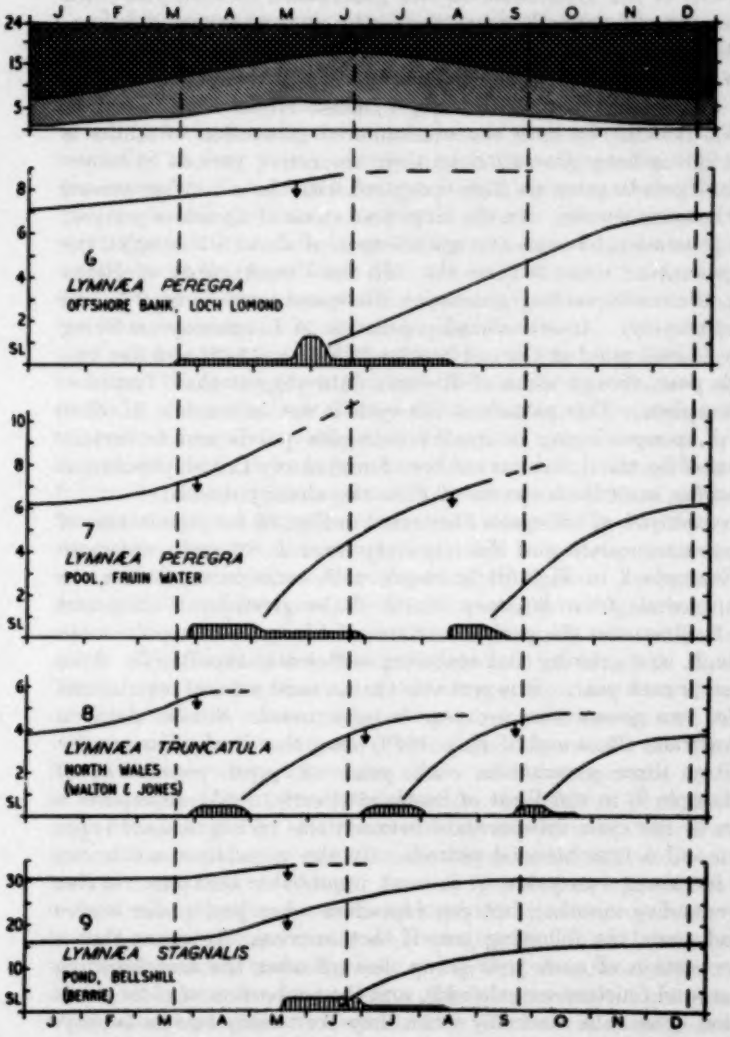

Fig. 9B

seasonal changes of mean shell size in populations, the onset of egg-laying (downward arrows), and lines mark the solstices and equinoxes, and the vertical size scales (which differ) are in millimetres. sunlight (light shading), and the average actual sunshine (white), the latter being based on mean where data for several years are available an overall mean is used. Examples **2**, **3**, **4**, **6** and **7** are and Jones (1926) and **9** from Berrie (1958).

of this paper, discussion of sample AQ46). One only of the populations of *Ancylus fluviatilis* in Windermere, studied by Geldiay (1956), shows this pattern of life cycle.

Another pattern of life cycle involves two generations in each year with complete replacement of a spring-born generation by an overwintering generation. In Figs. 9A & B this is illustrated by example **7** of a population of *Lymnaea peregra* living in a river pool near Loch Lomond (see § 6 of this paper), and by the population of *Physa* living at Botshol, Utrecht, Holland (example **5**), based on De Wit (1955). In both the overwintered generation of adults is larger than the spring-born generation at their respective periods of reproduction, and adult growth rates are high compared with those in other annual populations of the same species. In the river pool stock of *Lymnaea peregra*, the spring-born generation have an average life-span of about 4·5 months, the overwintering generation about 9·5 months. In the Utrecht stock of *Physa* (De Wit, 1955), the corresponding generation life-spans seem to be 3·5, and 10·5 months respectively. An introduced population of *L. catascopium* living in an artificially heated pond in Central Scotland (Kevan, 1943) also has two generations each year, though some of Kevan's data suggest that " replacement " is not complete. This pattern of life cycle is not uncommon in other populations of *L. peregra* living in smaller eutrophic ponds and in certain rivers in the West of Scotland, but has not been found in any British population of *Physa*, of *Ancylus*, or of those species of *Planorbis* already studied.

The last two examples of life cycles illustrated in Fig. 9B for populations of the small *Lymnaea truncatula* and the relatively large *L. stagnalis* are more exceptional. Example **8** in Fig. 9B is based, with some interpolation, on figures for *L. truncatula* from Anglesey, North Wales given by Walton and Jones (1926). It illustrates the probable course of life cycle in a pulmonate snail small enough, and growing and maturing sufficiently rapidly, for three generations to occur each year. It is probable that in most natural populations of *L. truncatula*, two generations per year is more usual. Similar data on *L. brazieri* in Australia (Ross and McKay, 1929) show that it also has usually two but possibly three generations each year. A pond population of *L. stagnalis* (example **9**) in the West of Scotland (Berrie, 1958), represents a stage in pattern of life cycle intermediate between the various *annual* types discussed above and a true biennial pattern. In this population snails can live and grow for about two years (it is most improbable that any survive beyond say twenty-five months), but can reproduce when just under twelve months old, and again the following year if they survive. It seems that a considerable proportion of each year group dies off after the first breeding season (i.e. at around fourteen months old), and the proportion of older snails in the population again falls markedly when they are twenty-two to twenty-three months old. Thus the proportion of snails which survive to breed in two successive years is small. The writer is indebted to Mr A. D. Berrie for providing the unpublished data on which the above statement and example **9** in Fig. 9B are based. Another freshwater pulmonate which can live more than two years is *Planorbarius corneus*. In its few habitats in Scotland (to which the species was probably introduced—Hunter, 1953 c ; McMillan, 1955), it

is probably a true biennial, breeding first when nearly two years old. In its more natural habitats in south-eastern England, the life cycle resembles that of *L. stagnalis* in example **9** above, and individual snails can breed in their first year (Boycott, 1936, and references therein).

A few generalizations can be made about these life cycles (Figs. 9A & B). 1—There is a minimum size (and a minimum mean size for the population) for the onset of breeding, but this can differ in different populations of certain species. 2—Growth usually continues after breeding. 3—Survival after breeding varies in different populations of each species. 4—A relatively high mortality in very young spat is common to all species. (This could not be represented in Figs. 9A & B, but see § 3 of this paper and also Hunter, 1953 a & b, 1961). 5—All species show reduced growth rates in winter and, except in certain populations of *L. peregra*, there is some winter period during which the mean size of the population does not increase. 6—In the examples studied, all egg-laying takes place in the summer six months of the year, i.e. between the lines marking the equinoxes in Fig. 9. (Note : No specific significance is attributed to the equinoxes, the two dates, 21 March and 23 September happen to delimit the season of temperatures suitable for reproduction over the habitats studied). Thus the time of onset of breeding in a population is dependent both on environmental factors, of which water temperature is by far the most important, and on endogenous causes involving the growth of the snails. Internally, maturation may involve the summed effects of the temperature and trophic conditions experienced by each snail during its life from hatching to copulation, but it is not entirely separable from the growth as there is a clear minimum breeding size for each species/population. In certain extreme cases, among the examples above, the actual onset of breeding is obviously determined, either by environmental temperature alone or by size and endogenous factors alone. This further determines the pattern of life cycle in the population. Thus, in several populations of *Lymnaea peregra*, the overwintering snails are mostly above the minimum breeding size for the species and show apparently mature reproductive organs. Therefore, egg-masses are produced shortly after the water temperatures rise above 9°C in late spring. On the other hand, in the population of *Planorbis albus* on the offshore bank in Loch Lomond (Fig. 9A, example **2**), at the time of the rise in water temperatures in spring the snails are all below minimum breeding size with little development of the female reproductive system. In this population, egg-production does not occur until July, after a considerable period of summer growth. The effects of environmental temperatures on reproduction have been more extensively studied in marine invertebrates, and both direct, short-term stimuli, and indirect (or summed) effects over a whole annual cycle are known. In these freshwater pulmonates, it is not unlikely that both immediate external temperatures and endogenous factors could affect the life cycle by way of a hormonal mechanism. This might involve a substance like diantlin, whose action on spawning in oysters has been known for some time (Nelson, 1936 ; Nelson & Allison, 1940). Alternatively it could depend on a neurosecretory mechanism such as affects spawning in the marine bivalves *Mytilus* and *Chlamys* (Lubet, 1955, 1956, 1957), and as exists in several gastropods (Tuzet *et al.*, 1957).

There is considerable interpopulation variation in adult mortality and, like the onset of breeding, this is likely to be determined partly by environmental, partly by endogenous factors. Growth is still continuing in adults when death occurs, but in most annual populations of freshwater snails the majority of the adults die soon after breeding. As Van Cleave (1934, 1935) first discussed, growth in many molluscs, in contrast to the process normal in arthropods and in vertebrates, is usually continuous throughout life and there is rarely cessation at maturity. The fact that in *Planorbis albus* and *Valvata piscinalis* those populations with relatively slower rates of growth show longer post-spawning survival of adult snails (see § 4 and § 7 above) suggests the occurrence to some extent of " endogenous senescence " (in the sense used by Comfort, 1956, 1957). In contrast, Hunter (1953 a, 1961) has emphasized the occurrence of apparent environmental limitations of growth in some species. In such snail populations as *Ancylus* in the Upper Craigton Burn, and *Lymnaea peregra* in the Loch Lomond littoral, there is discriminative selection of the larger adult snails in early summer (Hunter, 1953 a-b, and unpublished work). In typical highland stream populations of *Ancylus*, Hunter (1953 a) suggested that the environmental limitation of growth (and therefore of age) could depend on the rate of water flow and on the growth of algae attached to the shell. In populations of *Physa fontinalis* and *Lymnaea peregra* living in the littoral at Loch Lomond, environmental limitation of size could depend on the respiratory needs of the snails in the higher water temperatures of summer. Figures are given elsewhere (Hunter, 1953 d) of the proportionate decrease with growth in the surfaces available for cutaneous respiration in both these species. Thirdly, work on migrations in *L. peregra* (Hunter, 1953 b) showed that, under certain conditions, larger adult snails were more liable to a degree of starvation than were young snails in the same population. A critical size, above which adult death is more likely, is determined by environmental factors in each of these cases. The potential maximum life-span of these freshwater snails, which is probably controlled by internal senescence (as in Comfort, 1956, 1957) must be distinguished from the actual mean life-span in each population under natural conditions. The actual life-span in the wild is often not obviously affected by endogenous senescence but is subject to environmental limitation.

When the present paper was being completed, the important work of Duncan (1959) on the life cycle of *Physa fontinalis* became available. His main data were derived from a population in a pond at Stanmore, Middlesex, for which in some years the life cycle is essentially similar to that for the population of *Physa* inshore in Loch Lomond, although the Stanmore growth rates are higher and adult size greater. Other data from a population of *Physa* in Windermere indicate a simple annual life cycle like that found in this species on the offshore bank in Loch Lomond. In addition, Duncan provides behavioural analysis of the stimuli which initiate copulation and oviposition in *Physa*. His conclusions from this independently support the concept outlined above that the onset of the breeding season is dependent on the interaction of endogenous and external factors. There exist many accounts of life cycle in various freshwater snails in laboratory culture (e.g. see many references in Boycott, 1936 ; Noland & Carriker, 1946 ; De Wit, 1955 ;

Frömming, 1956), but the present discussion is deliberately limited to the results from field studies on natural populations.

These factors, termed endogenous above, affecting breeding or mortality, are probably in most cases phenotypic and reflect environmental conditions during the lifetime of the snail. However, certain interpopulation differences in the seasonal course of life cycle in *Lymnaea peregra* (see § 6 of this paper) seem likely to be genetically determined. For example, the Eriboll population, and some other highland populations of *L. peregra*, show the unusual combination of a high growth rate with mid-summer breeding, and hence a simple annual life cycle. Neither low water temperatures, nor insufficient size for spring maturity, can be responsible for the lateness of the breeding season, and some genetic factors in these must differ from other populations of *L. peregra* in determining this.

To recapitulate, several species of freshwater snails have basically a simple annual life cycle, but considerable infraspecific differences are found. In *Planorbis albus* and *Valvata piscinalis* such differences between populations involve only growth rates and the time and intensity of the breeding season. In *Physa fontinalis*, *Lymnaea peregra* and *Ancylus fluviatilis* interpopulation differences involve the seasonal course of the reproductive cycle (and the number of generations per year), as well as growth rates. In most cases, these interpopulation variations could be determined phenotypically by trophic or temperature differences in the environment, but certain infraspecific variation in *L. peregra* probably has a genetic basis.

GENERAL DISCUSSION

The extensive interpopulation differences in growth and reproduction which can occur within species of freshwater snails are connected with certain peculiarities of the environment provided by fresh waters. Hubendick (1952, 1954) and Hunter (1952, 1956, 1957) have pointed out independently, and from different bases, that the process of evolution in molluscs living in fresh waters has been markedly different from evolution in similar animals living in the sea or on land. This results from the transience of freshwater environments and the high degree of small-scale, short-term isolation which can occur within them. Most snail populations detailed in the present paper are relatively "stable", occurring in "good" habitats of unusual permanence (e.g. Loch Lomond). The majority of populations of freshwater snails live in bodies of water which are both more variable in extent and more transitory. In these less permanent habitats variations in growth rates and fecundity are probably even greater.

The selective advantages of an annual cycle, in which the adults do not survive long after breeding to compete for food with their offspring, are obvious. Extensive phenotypic plasticity in growth rates and fecundity is also of selective advantage in the maintenance of these populations. Even in relatively stable populations, considerable annual variation occurs in the size attained by, and in the densities of, adult snails at their breeding time, and this variation can be correlated with weather conditions prevailing during the preceding year (Hunter, 1961). The adaptive plasticity in reproduction, when combined with

an environmental cause of death at a critical size, will permit a population to compensate for these annual variations in the next generation. This will be of selective advantage in maintaining the size of the population. Quantitative assessment of the effects of such compensatory regulation is prevented by lack of adequate field data on total egg production in different conditions and in different years (see Hunter, 1961). Results from laboratory cultures (references above and in Bondesen, 1950) are of little value. Any discussion of life cycle and fecundity in pulmonate snails, particularly if rates of selection are being considered, must be based on field studies on natural populations. Elsewhere (Hunter, 1953 a, 1961) measurements of variation in growth and density in molluscan populations have been proposed as a possible means for assessment of annual and other variations in the total organic productivity of bodies of fresh water. The feasibility of this reflects the biological advantage that plasticity confers in allowing the maximum production of snail tissue, i.e. the optimum utilization of the varying environmental conditions, both trophic and physical, found in any body of fresh water. On the other hand, the actual pattern of life cycle, though varying within the species, seems to remain constant within each population.

The occurrence of populations showing differing but relatively constant patterns of life cycle environmentally evoked, together with a few populations in which one particular pattern seems genetically determined, is of evolutionary significance. It is comparable with the classic range of involute shell forms of *Lymnaea peregra* found in certain " highland " lakes in Ireland and Scotland. Laboratory breeding of these forms by Boycott (1938) showed that in may stocks the involute or a low-spired condition had been phenotypically determined by the environment, while in a few, the shell condition was genetically fixed. Field investigation of the distribution of the Irish forms (Huggins, 1918 ; Boycott, Oldham & Waterston, 1932) showed that each lake-population was constant in form and that this constancy persisted over many years. However, adjacent lakes could support quite different shell-forms, and correlation of the involute and other forms with specific ecological differences was not always clear. Opposed theories suggest (Waddington, 1953 a) that the genetically fixed involute stocks derive from those adaptively plastic, in which involution can be environmentally produced, or (Underwood, 1954) that facultative stocks derive from fixed ones (see also Waddington, 1953 b c, 1956 ; Warburton, 1956). The occurrence within a species of a particular characteristic, in many populations as an environmental modification, but in occasional populations genetically fixed, may be more general in freshwater molluscs than is thought. In addition to life cycle pattern, and shell characters, two types of egg-masses produced by different stocks of *L. peregra* may be determined environmentally in some cases, genetically in others (see § 6 above, and Hunter, 1961). It is possible that the famed abyssal lymnaeids of Swiss lakes (André, 1901 ; Roszkowski, 1912, 1914 a b) possess genetically fixed versions of characteristics which are now known to be widespread and phenotypically determined, in pulmonate populations living far offshore in lesser depths in other lakes, such as Loch Lomond (Hunter, 1953 d). Examples of the same form of a species, being in some cases genetically determined, and in others

resulting from phenotypic modification, are better understood in plants, such as the economically important but variable grass, *Dactylis glomerata*.

In general, adaptive plasticity of form and function is common in freshwater animals. Each case implies possession of a genotype which allows phenotypic flexibility. The characteristic plasticity of respiratory behaviour in freshwater pulmonate snails has been discussed elsewhere (Hunter, 1953 d, 1957). Similar plasticity of growth cycles and reproductive behaviour in some species of freshwater snails has been reported above. The type of selection occurring in fresh waters is a consequence of the nature of the environment. The transience of most freshwater habitats limits the number of generations for which any separate population of freshwater animals can exist. But, a high degree of short-term, small-scale isolation can occur, as freshwater habitats are geographically discontinuous and mostly of small extent. One result is that the limnic gastropods are characterized by little full speciation but much infraspecific variation (Hubendick, 1954 ; Hunter, 1957). It is now suggested that this adaptive plasticity found in respiration, in reproduction and in other aspects of the physiology of freshwater snails, is of fundamental selective value. In many species of freshwater pulmonates particularly, selection has produced genotypes which can show phenotypic flexibility. What appears to have been most strongly selected *for* is the capacity to vary—the possession of adaptive plasticity.

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SUMMARY

Within each species of freshwater snail, there are variations from population to population in growth rates, reproduction, and the course of life cycles. Using samples from Loch Lomond and elsewhere, data are presented on the seasonal changes of mean shell size in different populations, and on breeding and egg-production in them. Standards are provided by dredged samples of four species (the pulmonates : *Planorbis albus*, *Physa fontinalis* and *Lymnaea peregra*, and the prosobranch : *Valvata piscinalis*) from an isolated offshore bank in Loch Lomond, with poor feeding conditions. Seasonal changes in total density of snails on the bank, and in relative numbers of each species, are noted and related to breeding and subsequent recruitment of young snails to the populations. Comparative records of growth and annual cycle are provided from other populations of these four species. In discussing the interpopulation variations which occur, existing data on a fifth species, the limpet *Ancylus fluviatilis*, are also used.

Infraspecific differences between populations in *Planorbis albus* and *Valvata* involve only growth rates and the time and intensity of the breeding season. In *Physa*, *Lymnaea peregra* and *Ancylus*, interpopulation differences involve the seasonal course of the reproductive cycle (and the number of generations per year), as well as growth rates. Life cycles and growth rates found in freshwater prosobranchs are briefly summarized. For freshwater pulmonates, a comparative series of characteristic life cycles is drawn up and discussed. Two patterns of simple annual cycle are described: "spring breeding", with relatively little post-winter growth, and "late-breeding", involving summer growth of adults. Another basically annual pattern involves a second generation but without replacement: the second autumn breeding season providing only a small fraction of the overwintering stock. A fourth pattern involves two generations in each year, with complete replacement of a spring-born generation by an overwintering generation. All four patterns have been found in different populations of *Physa fontinalis* and of *Lymnaea peregra*. More exceptional life cycles involving three generations per year, and twice-breeding and true biennial cycles are also noted. Variations in the time of onset of breeding in populations (and thus the course of life cycle) are dependent both on environment factors, water temperature being most important, and on endogenous causes involving the growth of the snails. In certain extreme cases, the actual onset is obviously determined by environmental temperature alone, or by endogenous factors alone. Variation in adult mortality is also discussed, and several examples quoted involving apparent environmental limitation of growth, and therefore of age. Most of the infraspecific variations found can be explained as environmentally evoked, but certain interpopulation differences seem likely to be genetically determined.

Finally, some aspects of evolutionary significance are discussed, with reference to the temporal and spatial peculiarities of the freshwater environment. It is suggested that the adaptive plasticity found in respiration, in reproduction, and in other aspects of the physiology of freshwater snails, is of fundamental selective value. As regards pulmonate snails particularly, it appears that selection operating in the freshwater environment tends to produce genotypes which can show considerable phenotypic flexibility.

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